WARMING WINTERS AND CHANGING HABITATS: INTERACTIVE EFFECTS ON RAPTOR POPULATIONS AND IMPLICATIONS FOR CONSERVATION

By

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The following individuals read and discussed the thesis submitted by student Neil A. Paprocki, and they evaluated his presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

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DEDICATION

To my parents.

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ABSTRACT

Studies across multiple spatial and temporal scales will improve understanding of the drivers of global change including habitat degradation, invasive species, and climate change. How global drivers affect the ecology of wintering raptors in western North America and the Great Basin may have important implications for changes in distribution and abundance, and consequently population persistence. I examined the winter distributions of six western North America raptor species using Christmas Bird Count data from 1975-2011 to assess range shifts over time and in relation to temperature. Also, I considered whether population patterns within Bird Conservation Regions (BCR) were best explained by changes in distribution or changes over time. I used an historical dataset from 1991-1994 and current information from 2010-2012 to examine whether wintering raptor occupancy patterns were consistent with regional changes in distribution and climate or habitat conditions within a local management unit, the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA). All six wintering raptor distributions in western North American have shifted north over time and five of six raptor species tended to winter further north during warmer winters. Northward shifts were predictive for 39% of regional population indices, and locally I observed increased occupancy for most wintering raptors in the NCA despite continued habitat degradation. Three raptor species also changed their habitat use over time by using more or less agriculture or more areas dominated by invasive plants. Changes in habitat use may at least partially mediate their apparent response to climate change. Raptors may be

particularly responsive to warming winters because of life history flexibility, high competition for nesting sites that drives males to winter farther north, or both. Organisms with broad geographic ranges that are flexible in their habitat use stemming from changing landscapes appear better able to respond to global forces such as climate change. Our ability to manage bird populations within local bird conservation regions and management areas will fundamentally change as more species exhibit ecological changes in response to global change.

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INTRODUCTION

How do climate and habitat changes interact on a local and broader level to influence populations? Numerous studies have shown the effects of climate change on a variety of taxa including phenological (i.e. earlier breeding times; Gordo 2007) and distribution shifts (i.e. further north; Hitch and Leberg 2007). However, while scientists are beginning to understand the effects of climate change on the natural world, there is still little known about the actual management implications behind these effects, and how they may interact with habitat change. We as scientists need to move beyond the effects of climate change, and focus on understanding how we can manage for these effects and their implications. Focusing on large-scale changes because of anthropogenic activities is one important part of that. One such ecosystem undergoing rapid change because of anthropogenic activities is the sagebrush steppe of the Great Basin. These changes include habitat alteration via increased human development, invasion by exotic species such as cheatgrass (*Bromus tectorum*), and climate change.

Cheatgrass and other exotic annuals initially and successfully colonized the severely overgrazed and damaged sagebrush landscape around the turn of the twentieth century (Mack 1981, Yensen 1981). Invasion by these exotic plants may be the most damaging and long-lasting threat facing native shrub-steppe habitat and is interrelated to both fire management schemes and livestock grazing (D'Antonio and Vitousek 1992, Jones and Longland 1999). Combined with overgrazing, cheatgrass quickly spread as ranchers began setting fires to promote new growth (Yensen 1981). Native sagebrush habitat has a fire cycle of at least every 40-100 years, with long periods of succession and re-establishment needed for native seeds to take hold (Kochert and Pellant 1986,

Epanchin-Niell et al. 2009). Because cheatgrass dominated sites are 500 times more likely to burn than other habitat types (Yensen 1981), the fire-return interval has been increased to approximately 10 years (Epanchin-Niell et al. 2009). The increased fire frequency does not provide sufficient time for the native vegetation to recover between wildfire occurrences. This increased frequency of fire, coupled with overgrazing practices that leave native vegetation more susceptible to invasion (Jones and Longland 1999, Bock et al. 2007), led to approximately 25% of native sagebrush habitat in the Great Basin containing cheatgrass by 1999 (Epanchin-Niell et al. 2009). Cheatgrass is also more likely to invade areas that are close to agriculture, power lines, and roads (Bradley 2010).

Greater sage-grouse (*Centrocercus urophasianus*) have been championed as an umbrella species for protecting sagebrush ecosystems from the various threats they face (Rowland et al. 2006). However, because guilds and species differ in their response to environmental disturbances, it is worth investigating the effects of habitat loss and fragmentation on other guilds within the sagebrush ecosystem. In particular, diurnal raptors (*Accipitriformes, Falconiformes*) have long been known as an environmental indicator group given their high mobility and position at the top of the food chain (Sergio et al. 2006). Piute ground squirrels (*Spermophilus mollis*; formerly Townsend's ground squirrel *Spermophilus townsendii*), which are the main prey of several breeding raptor species, will feed on and use cheatgrass habitat when it is green (Yensen et al. 1992). However, while cheatgrass can be very productive in wet years, it senesces faster than native vegetation and will become inedible during dry years making the habitat very unstable for squirrel populations (Yensen et al. 1992). Similar to greater sage-grouse,

black-tailed jackrabbits (*Lepus californicus*) prefer native shrubs such as big sagebrush (*Artemisia tridentata*) while burned areas that are more susceptible to cheatgrass invasion contain less suitable habitat (Smith and Nydegger 1985, Knick and Dyer 1997). Less studied but still an important foundational prey group for raptors, mice and microtine rodents have reduced densities in areas of high habitat patchiness with increased distances between native shrubs (Feldhamer 1979, Hanser and Huntly 2006).

The sagebrush steppe of southwest Idaho and the Great Basin is home to large breeding and non-breeding populations of raptors that prey on a diversity of organisms (Kochert and Pellant 1986). Non-breeding, and more specifically, wintering raptors are much more difficult to study given they are not tied to a central location (i.e nest) and are highly mobile. This makes drawing inferences about the ecology of wintering raptors challenging, and therefore we know relatively little about the effects of climate and habitat change on raptors during this crucial time of temperature and food stress. Indeed, many species have higher mortality rates during winter (Mihoub et al. 2010, Elliot et al. 2011), while the effects of surviving winter can also carry over into breeding populations by reducing an individuals body condition at the start of the breeding season (Sherry and Holmes 1996, Wilson et al. 2011). How populations respond to climate and habitat change over time on a local, regional, continental, and global level will be vital to our understanding of how these populations should be managed at different spatial scales. For example, the sagebrush ecosystem will continue to be negatively impacted by climate change, cheatgrass invasion, and land use change, but the risk level associated with each other these threats differs by geographical location (Bradley 2010).

In Chapter 1 I present wintering raptor distribution and regional population trend data from the Christmas Bird Counts (CBCs) of western North American from 1975 to 2011. The goal of this study was to first determine if winter raptor distribution shifts in relation to climate change have occurred and then determine if population indices within Bird Conservation Regions (BCRs) were explained by any distribution shifts. I modeled the latitudinal center of a raptors' wintering distribution in relation to year and temperature while also modeling the population index within a BCR in relation to year and distribution. Population indices are a measure of relative abundance during a given winter within a BCR. This is the first study to examine distribution shifts in western North American raptors and to determine if regional population trends are explained by distribution shifts.

In Chapter 2 I present findings from an observational study I conducted on wintering raptors in the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) during the 2010-2011 winters combined with historical data from the 1991-1994 winters. The goal of this study was to assess if changes in raptor occupancy and habitat use over time were related to distribution shifts related to climate change or local habitat change. I modeled raptor occupancy at point count sites in relation to time period and habitat type to determine whether regional, local effects, or both influenced raptor occupancy in the NCA.

To conclude this thesis, I discuss how important it was for my study to assess winter raptor populations on multiple spatial scales and at two points in time. I also provide local and regional management recommendations for particular raptor species' given their responses to climate and habitat change. Given these results, future avenues of

research and management are explored that may aide in determining how raptor populations are fluctuating and responding to continued climate and habitat change.

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CHAPTER 1: DISTRIBUTION SHIFTS HELP EXPLAIN REGIONAL CHANGES IN WINTERING RAPTORS: IMPLICATIONS FOR INTERPRETING POPULATION TRENDS.

Abstract

Studies of multiple taxa across broad-scales suggest that species distributions are shifting poleward in response to global climate change. Understanding the influence of distribution shifts on regional population indices will be an important part of interpreting population trends within local management units because, compared to a time when distribution were less dynamic, changes in population indices may be less likely to reflect local environmental conditions. I examined the latitudinal center of abundance for the winter distributions of six western North America raptor species using Christmas Bird Counts from 1975-2011. I predicted that birds wintered further north during warmer winters and that winter raptor distributions have shifted north over time. Also, I considered whether population indices within North American Bird Conservation Regions (BCR) were explained by distribution shifts. All six wintering raptors shifted their distributions north over time and five of six raptor species tended to winter further north during warmer winters. Northward shifts explained 44% of regional population trends emphasizing the importance of understanding how distribution shifts and population indices interact on a regional scale. Raptors may be particularly responsive to warming winters because of flexible migration behavior, high intraspecific competition for nesting sites that drives males to winter farther north, or both. If population-level

processes are driving distributional changes, then trends within some management units may not reflect changes in local habitat suitability. The ability to manage bird populations within local bird conservation regions will fundamentally change as more species experience changes in distribution in response to global climate change.

Introduction

Animal distribution shifts in relation to climate change have been well documented (Leech and Crick 2007, Doswald et al. 2009, DesGranges and Morneau 2010) with many comparative studies focusing on a large number of taxa across a broad geographic area (Hitch and Leberg 2007, La Sorte and Thompson 2007, Huntley et al. 2008). While this large-scale, inclusive approach advances our understanding of distribution shifts in a broad sense, rate of change estimates may depend on species- or population-specific life histories (Both and Visser 2001, Visser et al. 2003, Végvári et al. 2010), geography (Gordo et al. 2005, Hulbert and Lang 2012), or regional climate change patterns (Saether et al. 2003).

Examining distribution shifts on a biologically relevant scale may contribute to a better understanding of population change over the same time period. As species distributions shift, long-term monitoring projects will likely detect changes in population index estimates. Indeed, avian wintering studies have found differing regional population trends at the Bird Conservation Region (BCR) level (Link et al. 2006, Sauer et al. 2008). Link et al. (2006) found regionally specific population trends in American Black Ducks (*Anas rupripes*) with population increases in northern regions and population declines in central and southern regions, while overall population indices remained stable. These regional population trend differences may be difficult to interpret, but could be partly

explained by distribution shifts since overall population indices remained stable over time. Bart et al. (2007) examined the population trends of wintering North American shorebirds and attempted to explain regional population trends. They concluded that wintering population declines were most likely a result of declining breeding populations, but they could not rule out the possibility of changing shorebird movements explaining the observed population declines. Warmer winters may allow birds to winter closer to, or stay on nesting grounds and birds may benefit from early arrival at nesting sites by securing higher quality territories (Drent et al. 2006, Berthold et al. 2005, Heath et al. 2012).

Many raptors are monitored with migration and non-breeding bird surveys because it is difficult to adequately sample breeding birds (Dunn et al. 2005). Raptors may be particularly responsive to warming winters because of their flexible migration behavior, high intraspecific competition for quality nest sites that drives protandry (earlier male arrival to breeding areas than female), or both (Espie et al. 2000, Heath et al. 2012). In addition, raptor distribution shifts may vary regionally because many species have strong north-south patterns of migratory connectivity (Hoffman et al. 2002) and weaker east-west population connectivity. Individual species of raptors may also vary in their response to climate change patterns given that projected changes are greatest at higher latitudes. Several raptor species breed at arctic latitudes exclusively (Bechard and Swem 2002), while other species' ranges encompass arctic and temperate regions (Kochert et al. 2002) or only temperate regions (Steenhof 1998). Finally, climate change patterns vary with distance from the coast (Intergovernmental Panel on Climate Change

2007), and this may also correspond to regional differences in distribution responses given the widespread, continental distribution of most raptor species.

I selected six raptor species that are common in western North America, highly detectable in surveys, and whose wintering distribution is fairly well sampled by Christmas Bird Counts (CBC): American kestrels (*Falco sparverius*), golden eagles (*Aquila chrysaetos*), northern harriers (*Circus cyaneus*), prairie falcons (*Falco mexicanus*), red-tailed hawks (*Buteo jamaicensis*), and rough-legged hawks (*Buteo lagopus*). My objectives were to investigate species-specific shifts in western North America wintering distributions over time and in relation to climate change and to compare these rates of shift to continental estimates, and assess whether distribution shifts accounted for regional population trends. I predicted that most raptor species would show a northern shift in their latitudinal center of abundance while also wintering further north during warm winters. I also predicted that some population indices within Bird Conservation Regions (BCRs) would be best explained by distribution shifts.

Methods

I used North American CBC data (National Audubon Society 2012) to evaluate distribution shifts and population trends for western North America raptors. I selected the CBC circles from the central 95% of the latitudinal distribution of each species' wintering range. The northern study area boundaries ranged from 51.2 to 53.5°N, and southern boundaries ranged from 27.8 to 31.9°N. I selected longitudinal divides based on banding and recovery data from the North American Bird Banding Program and previous studies of raptor flyways (Hoffman et al. 2002). Northern harriers and American kestrels rarely migrated across the Rocky Mountains so we selected the continental divide as their

eastern range boundary. Red-tailed hawks and rough-legged hawks were generally north-south migrants, and we chose the eastern edge of the Rocky Mountains as their eastern range boundary (102.0°W) to incorporate all three (Pacific, Intermountain, Rocky Mountain) western North American migratory flyways (Hoffman et al. 2002). Golden eagles and prairie falcons were generally restricted to the western United States and Great Plains region during winter (Steenhof et al. 2005), and I chose 95.0°W, roughly the eastern border of Oklahoma and Kansas, as their eastern range boundary.

I used CBC data from 1975 to 2011 because reporting of observer effort became relatively consistent after 1975 (La Sorte and Thompson 2007). CBC surveys were conducted by Audubon volunteers that surveyed a circular area with a radius of 12 km for 24 h during a two week period around 25 December. I modified La Sorte and Thompson's (2007) approach of selecting circles sampled at least once during a minimum of 9 of 12, 3-year time periods (e.g., 1975-1977, 1978-1980, …, 2008-2011; Table 1.1) to ensure adequate sampling. The 2008-2011 time-period contained four survey years. I included CBC circles even if a species was not detected in a given survey year unless an individual of a specific species was never counted on a circle. I removed data from select circles during years when zero or aberrant observer effort or raptor count data was present (n = 319, Peterson 1995).

I obtained continental estimates of distribution shifts from La Sorte and Thompson (2007; Appendix A) for all species except golden eagles, which were not analyzed. I estimated the annual latitudinal center of abundance for each species' wintering distribution (La Sorte and Thompson 2007). I calculated effort-corrected counts for each species because effort is not constant over the history of a CBC circle and

observer-count relationships were likely to be species-specific (Link and Sauer 1999). I converted the raw count and effort data to the log scale following previous work (Link and Sauer 1999) and then assessed the relationship between count and effort. A quadratic relationship between count and effort was the best fit for all species, however the nature of this relationship varied by species. I used the following effort-corrected count to calculate the weighted center of latitudinal abundance following La Sorte and Thompson (2007):

$$\frac{\log Count}{\left((\beta 1 \times \log Effort) + (\beta 2 \times \log Effort^2)\right)}$$

I calculated CBC-based population trends for individual BCRs within a species western wintering range. BCRs with ≤100 total surveys years, corresponding to ≤3 CBC circles within the BCR, were merged with neighboring BCRs containing >100 total survey years (see Table 1.2) to avoid difficulties with model convergence characteristic of small sample sizes. While choosing to merge BCRs with ≤100 total survey years was arbitrary, I do not think this biased the results of my study. The Sierra Nevada and BCRs along a species range boundary were most often merged to increase sample sizes. I examined overall population trends to determine if this was correlated with any observed distribution shifts and to determine if trends within BCRs were representative of the entire study area.

I obtained regional climate data in the form of daily minimum air temperature anomalies from the Global Historical Climatology Network gridded dataset (HadGHCND; http://www.ncdc.noaa.gov/oa/climate/ghcn-daily/; Casesar et al. 2006). The use of anomaly values versus recorded temperatures allowed for a standardized representation of climate change across a variety of locations with different minimum

temperatures (Heath et al. 2012). I chose grid locations within the HadGHCND from a species breeding range within our species-specific longitudinal CBC divide (e.g. breeding range arctic grid cells west of 102°W for rough-legged hawks). I averaged daily minimum air temperature anomalies for each wintering period prior to when most CBCs are surveyed, 15 November – 31 December from 1974 to 2010, to represent annual winter minimum temperatures.

Statistical Analysis

For all analyses I used general linear models and an information-theoretic approach with second-order Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002). For wintering distribution analyses I created independent models for the latitudinal center of abundance for each species. I assessed the linear fit of the predictor variable temperature on the center of abundance prior to model selection and used the best fit for all further analyses. *A priori* predictor variables included scaled year and mean annual minimum air temperature anomaly. I calculated Pearson correlations between year and temperature for each species to check for multicollinearity in the same model set (Table 1.1). If a Pearson correlation was above 0.7 then I removed the least biologically relevant variable from the set.

For population trend and BCR analyses I created independent models for yearly effort-corrected count for each species. Predictor variables included in models were year, BCR, and the interaction between year and BCR. After finding a significant interaction between year and BCR for all species, I used BCR-specific linear models with the independent variable year to predict effort-corrected counts. I assessed the linear fit of year on count for each BCR to determine any quadratic trends in population change. I

examined whether regional population indices were best explained by distribution shifts or change over time by comparing evidence from linear models with the annual latitudinal center of abundance and year (change over time) as predictor variables. Year and annual latitudinal center of abundance were correlated and not included in the same model.

For each model in a given set, I calculated an AIC_c value along with an Akaike Weight (Burnham and Anderson 2002). For each latitudinal center of abundance model including year, temperature, or both in a set, I summed the weights to produce a weight of relative importance for that set (Lavoue and Droz 2009). I calculated 85% confidence intervals for parameter estimates to be compatible with an AIC approach (Arnold 2010). All other distribution and population trend estimates are presented as means ± SE unless otherwise noted. All statistical analyses were run with software from the R Development Core Team (2011).

Results

Pearson correlations between year and temperature in all distribution models ranged from 0.20 to 0.34 indicating a weak positive association between year and minimum temperature anomaly. Models including year as the predictor of the latitudinal center of abundance received the most support for all species and the relative weight of evidence for a year effect was high (>0.90; Table 1.2). All species showed evidence for a shift north in the latitudinal center of abundance over time (Fig. 1.1), however the degree of northward shift I observed varied from continental estimates (La Sorte and Thompson 2007, Table 1.1). This distribution shift ranged from 66.2 ± 11.9 km north for northern harriers to a 254.5 ± 22.2 km shift north for rough-legged hawks. Temperature was

positively associated with the latitudinal center of abundance for American kestrels, golden eagles, northern harriers, red-tailed hawks, and rough-legged hawk (Table 1.1), although the relationship was relatively weak compared to year. There was little evidence for this relationship in prairie falcons (Table 1.1).

One explanation for an apparent northern shift in distribution may be that the locations of CBC circles have shifted north over time. However, because I only included long-term circles surveyed in at least 9 of 12, 3-year time periods there was no correlation between year and latitude of CBC circles (northern harriers and American kestrels: r = 0.01, df = 7,142, P = 0.26; rough-legged hawks: r = 0.02, df = 9,847, P = 0.11; red-tailed hawks: r = 0.02, df = 9,513, P = 0.12; golden eagles: r = 0.01, df = 13,628, P = 0.36; prairie falcons: r = 0.01, df = 13,499, P = 0.36).

Relationships between regional population indices, winter distributions, or time depended on species and BCR. There was evidence that distribution shifts explained regional population indices in golden eagles, northern harriers, and rough-legged hawks (Table 1.3). Alternatively, changes over time best explained regional population indices for American kestrels, prairie falcons, and red-tailed hawks (Table 1.3). Across all species, 38% of the overall model weights provided evidence for population changes over time, while 44% of the overall model weights provided evidence for distribution shifts. The remaining 18% of model weights provided no evidence for either (Table 1.3). For all species except rough-legged hawks a quadratic trend estimating overall winter population changes from 1975 to 2011 provided the best model fit (Fig. 1.1). These include negative quadratic relationships for golden eagles, northern harriers, prairie falcons, and red-tailed hawks and a positive quadratic relationship for American kestrels. Rough-legged hawks

showed a negative linear overall population trend, however this may have been caused by a lack of adequate sampling of northern populations as I found evidence for a negative relationship between the yearly latitudinal center of abundance and yearly average abundance. In other words, as rough-legged hawk distributions shift poleward, the ability to monitor the wintering population of birds decreases because of CBC survey limitations.

Discussion

All six raptor species showed a shift north in their western winter distributions. This is consistent with results from continental studies on wintering birds (La Sorte and Thompson 2007). However, my findings differ in the degree to which raptors have shifted north. For species that I was able to directly compare with La Sorte and Thompson's (2007) findings, I found larger northern distribution shifts for American kestrels, prairie falcons, and rough-legged hawks and smaller shifts for northern harriers and red-tailed hawks. My findings highlight the need to focus on regional populations as they may experience different climate change patterns (Intergovernmental Panel on Climate Change 2007).

I also found evidence for five of the six species wintering further north during warm winters supporting results reported in the northeastern United States (Zuckerberg et al. 2011). However, an alternative explanation for an apparent northern shift in wintering distributions is differential land-use change in southern regions contributing to southern habitat loss effectively "pushing" raptors further north to areas that have not experienced as much habitat loss (Zuckerberg et al. 2011). Although I cannot rule out this explanation, my results show support for temperature contributing to raptors wintering

further north (Table 1.1). However, there was a strong year effect in the center of abundance models with temperature indicating there were other variables affecting the change in distribution. Anthropogenic factors such as increasing human populations and development should not be overlooked when assessing causes of range shifts (Zuckerberg et al. 2011). Other variables not assessed in this study that could influence raptor distribution include differential habitat loss, prey distribution and abundance, snow cover, precipitation, and other weather variables (Tingley et al. 2009, Zuckerberg et al. 2011).

There are several possible explanations for why raptors are shifting their winter ranges further north. As demonstrated in my study, warmer winter temperatures partly predict wintering further north, but this is not the only variable influencing range shifts given its low relative importance to year. Several previous studies have demonstrated decreased migration distances in American kestrels (Goodrich et al. 2012, Heath et al. 2012) associated with warming temperatures. Decreased migration distances, migratory "short-stopping", and increased winter residency are all possible explanations for my observed distribution shifts. It is advantageous for raptors to decrease their migration distances and winter further north or to stay on breeding grounds through the winter because early arrival to the breeding grounds can positively predict territory quality and reproductive success in species such as prairie falcons (Steenhof et al. 2005), merlins (*Falco columbarius*; Espie et al. 2000) and American Kestrels (Strasser 2010).

Distribution shifts, changes in population size, or both may explain regional population indices. I found evidence that distribution shifts explained some regional population indices of rough-legged hawks, golden eagles, and northern harriers. Approximately 75% of rough-legged hawk BCR population indices were explained by

distribution shifts. Rough-legged hawks and golden eagles also had the largest northward distribution shifts and had the largest parameter estimates for the effects of minimum temperature on center of abundance. If temperature functions as a mechanism influencing migratory distance (Visser et al. 2009), then I would expect to see those species most affected by temperature changes to show the most evidence for distribution shifts. Population trends in northern BCRs increased while trends in southern BCRs decreased, providing less direct evidence that distribution shifts explained regional population indices. However, this pattern was not always indicative of distribution shifts driving population trends. For example, American kestrels showed similar increases in northern BCRs and decreases in southern BCRs, however, there was little evidence that these trends were explained by distribution, with the exception of the Great Basin BCR.

I found evidence that for some regions, changes in population indices were best explained by time. A little less than half of the American kestrel and red-tailed hawk BCR population indices showed population changes over time. The BCRs showing the most consistent support for population indices explained by time across species included the Great Basin, Badlands and Prairies, Shortgrass Prairie, and Central Mixed-grass Prairie BCRs. Data on breeding populations could provide additional evidence that population changes explained regional population indices. However, evidence on breeding populations is extremely difficult to obtain for many species whose breeding ranges extend into Canada and the high arctic where fewer long-term breeding surveys are conducted (Booms et al. 2010). Another difficultly in connecting breeding population changes to wintering distributions and populations is the inability to accurately know from which areas wintering birds originate. I did not attempt to explain changes in

wintering distributions and populations from data on breeding raptors because of these difficulties.

Evidence for distribution shifts or changes in population size over time explaining regional population indices varied by species and by geographic location of BCRs. Golden eagles and rough-legged hawks have extensive arctic breeding populations and both provided the most support for distribution shifts explaining regional population indices suggesting long-distance arctic migrants may be more likely to experience distribution shifts that influence regional population indices. At the BCR level, the Great Basin and Great Plains BCRs provided the most evidence for population changes explaining regional population indices while the Prairie Potholes and southern most regions, including the Coastal California, Sonoran and Mohave Deserts, Sierra Madre Occidental BCRs, provided the most evidence for distribution shift explaining population indices. All other BCRs provided either little or substantial evidence for both modes explaining population indices.

These results further demonstrate the importance of viewing distribution shifts on a species-specific and regional, instead of continental, level. In light of this land managers may better focus their conservation efforts away from regional areas experiencing winter population declines caused by distribution shifts. For instance, I found evidence for golden eagles, prairie falcons, and rough-legged hawks experiencing winter population declines in some southern BCRs where indices were best explained by distribution shifts. Without an understanding of range-wide distribution shifts, land managers could misinterpret these declines and attempt to improve habitat or other environmental conditions. If the entire range of a species has shifted further north, no

amount of habitat restoration will compensate for the improved climatic conditions now found further north. In regions experiencing declines not caused by distribution shifts, additional research should focus on determining causes behind wintering population declines and how we can mitigate for them. Finally, I observed several instances of model selection uncertainty between our two competing modes of regional population change. This was observed most often in golden eagles and demonstrates the difficultly in separating these in species with complex migratory patterns (Hoffman and Smith 2003). Prairie falcons also exhibit complex migratory patterns (Steenhof et al. 2005) and are generally counted at low densities at migration stations and on Breeding Bird Survey routes (Hoffman and Smith 2003), making statistical inference difficult. Given this, and the inability to clearly differentiate between distribution shifts or actual population changes explaining regional population indices, continued monitoring of prairie falcon breeding populations and movement patterns is critical.

An apparent decline in overall population size could result if some northern wintering populations are not effectively sampled in our analysis or by a lack of adequate sampling in extreme northern locations by CBC circles. If winter distributions have shifted so far north that they are now outside of the CBC sampling area, I would expect to see evidence for a decline in wintering populations. I saw evidence for this in only one of the six-raptor species: rough-legged hawks. This suggests that the apparent western population decline I observed in rough-legged hawks may be because of an inadequately sampled northern wintering population. Perhaps this area is not adequately sampled by the CBC or was eliminated by my analysis method. However, I know of no other study that has assessed rough-legged hawk populations directly. Moreover, little to no research

has been conducted on rough-legged hawk breeding populations in the past two decades (Swem 1996) to help test my hypothesis of a stable western wintering population moving north. Rough-legged hawks may be a model species for how climate change can impact distributions, populations, and movements given their extensive arctic breeding range and the large winter distribution shift documented in this study.

Future studies and analyses of wintering raptors in the western United States should attempt to explore how human population growth and change are influencing distribution shifts and regional population trends. Teasing apart climate, human populations, and distribution shifts may be difficult as human population growth tends to be highest in warmer, southern areas such as California and Arizona that exhibit declining raptor population trends not caused by distribution shifts. As the global climate continues to warm, species wintering ranges may continue to shift further north. As a consequence, land managers in northern regions may become increasingly responsible for managing a higher proportion of a species wintering population. This will have implications for future population persistence given the importance of winter survival on avian population demographics.

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Table 1.1. The number of Christmas Bird Count circles (Num. CBCs), continental estimates for the effect of year on latitude center of abundance (Continental Lat. CA; from La Sorte and Thompson 2007), and parameter estimates with 85% confidence intervals (7.5^{th} – 92.5^{th} percentiles) for the effect of year and minimum temperature anomaly (Temp) used to explain winter distributions of six raptor species from 1975 to 2011 in western North American using Christmas Bird Counts. The continental estimate of change in latitude center of abundance was not available for golden eagles.

Species	Num. CBCs	Continental Lat. CA	Latitude Center of Abundance	
		Year	Year[a]	Temp[b]
American kestrel	211	0.44	1.90 (1.57, 2.31)	4.16 (1.15, 7.16)
golden eagle	353		5.22 (4.54, 5.89)	16.94 (8.68, 25.20)
northern harrier	212	3.94	1.79 (1.33, 2.25)	4.93 (1.88, 7.97)
prairie falcon	330	1.03	2.21 (1.52, 2.91)	3.76 (-4.02, 11.55)
red-tailed hawk	295	6.95	3.33 (2.97, 3.68)	6.70 (1.19, 12.20)
rough-legged hawk	279	5.94	6.88 (6.02, 7.74)	10.90 (2.37, 19.43)

[a] = all year estimates are in km yr-1; [b] = all temperature estimates are in km °C-1.

Table 1.2. Model sets for predicting the latitude center of abundance in relation to year and annual minimum temperature anomaly (temp) for six wintering raptor species from 1975 to 2011 in western North America using Christmas Bird Counts; k = number of parameters. Models are ordered according to the support received from Akaike's information criterion (AIC_c) and from Akaike weights (w_i); $\Delta AIC = AIC_{ci}$ – minimum AIC_c.

Species	Model	k	AIC_c	ΔAIC	w_i
American kestrel	year	3	-38.86	0.00	0.53
	year + temp	4	-38.59	0.28	0.47
	temp	3	-2.75	36.11	0.00
	null	2	-1.15	37.71	0.00
golden eagle	year + temp	4	11.92	0.00	0.72
	year	3	13.78	1.87	0.28
	temp	3	61.57	49.65	0.00
	null	2	67.42	55.50	0.00
northern harrier	year + temp	4	-15.42	0.00	0.55
	year	3	-15.05	0.37	0.45

	temp	3	3.56	18.99	0.00
	null	2	6.53	21.95	0.00
prairie falcon	year	3	16.09	0.00	0.78
	year + temp	4	18.61	2.52	0.22
	null	2	31.07	14.98	0.00
	temp	3	32.93	16.85	0.00
red-tailed hawk	year	3	-33.43	0.00	0.72
	year + temp	4	-31.54	1.90	0.28
	temp	3	30.76	64.19	0.00
	null	2	31.49	64.92	0.00
rough-legged hawk	year	3	31.52	0.00	0.78
	year + temp	4	34.05	2.52	0.22
	temp	3	86.30	54.78	0.00
	null	2	87.34	55.82	0.00

Table 1.3. Delta AIC_c and Akaike weights (in parentheses) for separate models including the effect of distribution shifts (Shift) or change over time (Year) explaining Christmas Bird Count population indices within Bird Conservation Regions for western North American raptors. Models with the highest weight in a model set are in bold. (-) indicate Bird Conservation Regions for each species outside of the wintering range analyzed in this study. See footnotes for combined Bird Conservation Regions because of insufficient samples sizes.

Species	Models	Northern Pacific Rainforest	Great Basin	Northern Rockies	Prairie Potholes	Sierra Nevada	Southern Rockies/Colorado Plateau	Badlands and Prairies
American kestrel	Shift	5.2 (0.07)	**0.0 (0.85)[a]**	1.3 (0.28)	-	-	8.1 (0.02)	-
	Year	**0.0 (0.93)**	3.4 (0.15)	2.0 (0.19)	-	-	**0.0 (0.98)**	-
	Intercept	15.5 (0.00)	41.0 (0.0)	**0.0 (0.53)**	-	-	14.3 (0.00)	-
northern harrier	Shift	**0.0 (0.45)**	13.8 (0.00)	**0.0 (0.83)**	-	0.4 (0.34)	0.9 (0.25)	-
	Year	0.4 (0.37)	**0.0 (1.00)**	4.9 (0.07)	-	1.0 (0.25)	0.2 (0.35)	-
	Intercept	1.8 (0.18)	29.7 (0.00)	4.3 (0.10)	-	**0.0 (0.41)**	**0.0 (0.40)**	-
rough-	Shift	**0.0 (0.52)**	**0.0 (0.98)[b]**	1.4 (0.32)	**0.0 (0.77)[c]**	-	**0.0 (1.00)**	3.0 (0.19)

legged hawk	Year	0.2 (0.48)	8.4 (0.01)	**0.0 (0.66)**	2.4 (0.23)	-	12.0 (0.00)	**0.0 (0.81)**
	Intercept	36.0 (0.00)	9.9 (0.01)	7.4 (0.02)	22.6 (0.00)	-	33.7 (0.00)	33.9 (0.00)
red-tailed hawk	Shift	**0.0 (0.99)**	14.6 (0.00)	10.1 (0.01)	-	1.2 (0.28)	0.5 (0.43)	4.2 (0.11)[d]
	Year	10.1 (0.01)	**0.0 (1.00)**	**0.0 (0.99)**	-	1.7 (0.22)	**0.0 (0.57)**	**0.0 (0.89)**
	Intercept	38.4 (0.00)	73.7 (0.00)	48.6 (0.00)	-	**0.0 (0.50)**	30.2 (0.00)	27.4 (0.00)
prairie falcon	Shift	0.5 (0.37)	6.3 (0.04)[e]	**0.0 (0.94)**	1.4 (0.33)	-	2.0 (0.21)	1.6 (0.20)
	Year	2.2 (0.16)	**0.0 (0.95)**	6.6 (0.03)	**0.0 (0.67)**	-	**0.0 (0.57)**	0.5 (0.35)
	Intercept	**0.0 (0.47)**	8.9 (0.01)	7.0 (0.03)	14.1 (0.00)	-	1.9 (0.22)	**0.0 (0.45)**
golden eagle	Shift	2.2 (0.20)	**0.0 (0.78)**	2.2 (0.25)	**0.0 (0.69)**[f]	2.1 (0.21)	2.4 (0.19)	**0.0 (0.87)**
	Year	2.4 (0.19)	3.4 (0.14)	**0.0 (0.75)**	1.6 (0.31)	2.3 (0.19)	2.3 (0.19)	4.2 (0.11)
	Intercept	**0.0 (0.61)**	4.8 (0.07)	11.9 (0.00)	9.3 (0.01)	**0.0 (0.60)**	**0.0 (0.62)**	7.6 (0.02)
Overall	Shift	**0.43**	0.44	0.44	**0.60**	0.28	0.35	0.34
	Year	0.36	**0.54**	**0.45**	0.40	0.22	**0.44**	**0.54**
	Intercept	0.21	0.01	0.11	0.00	**0.50**	0.21	0.12

[a] = Sierra Nevada merged with Great Basin; [b] = Sierra Nevada merged with Great Basin; [c] = Boreal Taiga Plains merged with Prairie Potholes; [d] = Boreal Taiga Plains and Prairie Potholes merged with Badlands and Prairies; [e] = Sierra Nevada merged with Great Basin; [f] = Boreal Taiga Plains merged with Prairie Potholes

Table 1.3 continued.

Central Mixed-grass Prairie	Oaks and Prairies	Eastern Tallgrass Prairie	Coastal California	Sonoran and Mohave Deserts	Sierra Madre Occidental	Chihuahuan Desert	Gulf Coast Prairie	Average Weight
-	-	-	29.0 (0.0)	1.9 (0.22)	0.7 (0.29)	-	-	0.25
-	-	-	**0.0 (1.0)**	2.2 (0.19)	**0.0 (0.42)**	-	-	**0.55**
-	-	-	47.9 (0.0)	**0.0 (0.59)**	0.8 (0.28)	-	-	0.20
-	-	-	0.5 (0.37)	0.9 (0.32)	1.4 (0.27)	-	-	**0.35**
-	-	-	2.1 (0.16)	2.4 (0.16)	2.3 (0.17)	-	-	0.32
-	-	-	**0.0 (0.47)**	**0.0 (0.52)**	**0.0 (0.56)**	-	-	0.33
-	-	-	**0.0 (1.00)**	**0.0 (1.00)**	**0.0 (0.97)**	**0.0 (0.96)**	-	**0.79**
-	-	-	23.4 (0.00)	13.2 (0.00)	7.0 (0.03)	6.1 (0.04)	-	0.21
-	-	-	49.8 (0.00)	37.9 (0.00)	19.2 (0.00)	23.8 (0.00)	-	0.00
-	-	-	**0.0 (0.71)**	**0.0 (0.82)**	**0.0 (0.73)**	4.0 (0.11)	-	0.38

-	-	-	2.0 (0.26)	3.0 (0.18)	2.0 (0.27)	**0.0 (0.87)**	-	**0.57**
-	-	-	6.5 (0.03)	14.4 (0.00)	13.9 (0.00)	7.7 (0.02)	-	0.05
3.1 (0.17)	2.2 (0.16)[g]	2.2 (0.20)[h]	**0.0 (0.64)**	3.4 (0.10)	**0.0 (0.63)**	1.9 (0.20)	-	0.30
0.0 (0.81)	0.9 (0.33)	2.4 (0.19)	3.1 (0.14)	**0.0 (0.56)**	1.1 (0.37)	1.1 (0.30)	-	**0.45**
7.2 (0.02)	**0.0 (0.51)**	**0.0 (0.61)**	2.1 (0.22)	1.1 (0.33)	17.2 (0.00)	**0.0 (0.50)**	-	0.25
0.5 (0.43)	0.3 (0.46)[i]	0.9 (0.30)	**0.0 (0.73)**	**0.0 (0.56)**	**0.0 (0.89)**	0.1 (0.42)	2.3 (0.19)	**0.48**
0.0 (0.57)	**0.0 (0.53)**	1.6 (0.22)	3.6 (0.12)	0.5 (0.43)	4.7 (0.09)	2.2 (0.15)	2.4 (0.19)	0.28
21.9 (0.00)	9.3 (0.01)	**0.0 (0.48)**	3.2 (0.15)	11.6 (0.00)	7.2 (0.02)	**0.0 (0.44)**	**0.0 (0.62)**	0.24
0.30	0.31	0.25	**0.58**	**0.50**	**0.63**	**0.42**	0.19	**0.44**
0.69	**0.43**	0.21	0.28	0.25	0.23	0.34	0.19	0.38
0.01	0.26	**0.55**	0.15	0.26	0.14	0.24	**0.62**	0.18

[g] = Edwards Plateau, West Gulf Coastal Plain/Quachitas, and Tamaulipan Brushlands merged with Oaks and Prairies; [h] = Prairie Hardwood Transition merged with Eastern Tallgrass Prairie; [I] = Edwards Plateau, West Gulf Coastal Plain/Quachitas, and Tamaulipan Brushlands merged with Oaks and Prairies.

Figure 1.1. The relationship between year and latitudinal center of abundance (° latitude), winter minimum temperature anomaly (°C) and latitudinal center of abundance, and year and effort corrected count for American kestrels, golden eagles, northern harriers, prairie falcons, red-tailed hawks, and rough-legged hawks in western North American Christmas Bird Counts from 1975 to 2011. Presence of a line indicates a predictive relationship.

Figure 1.1.

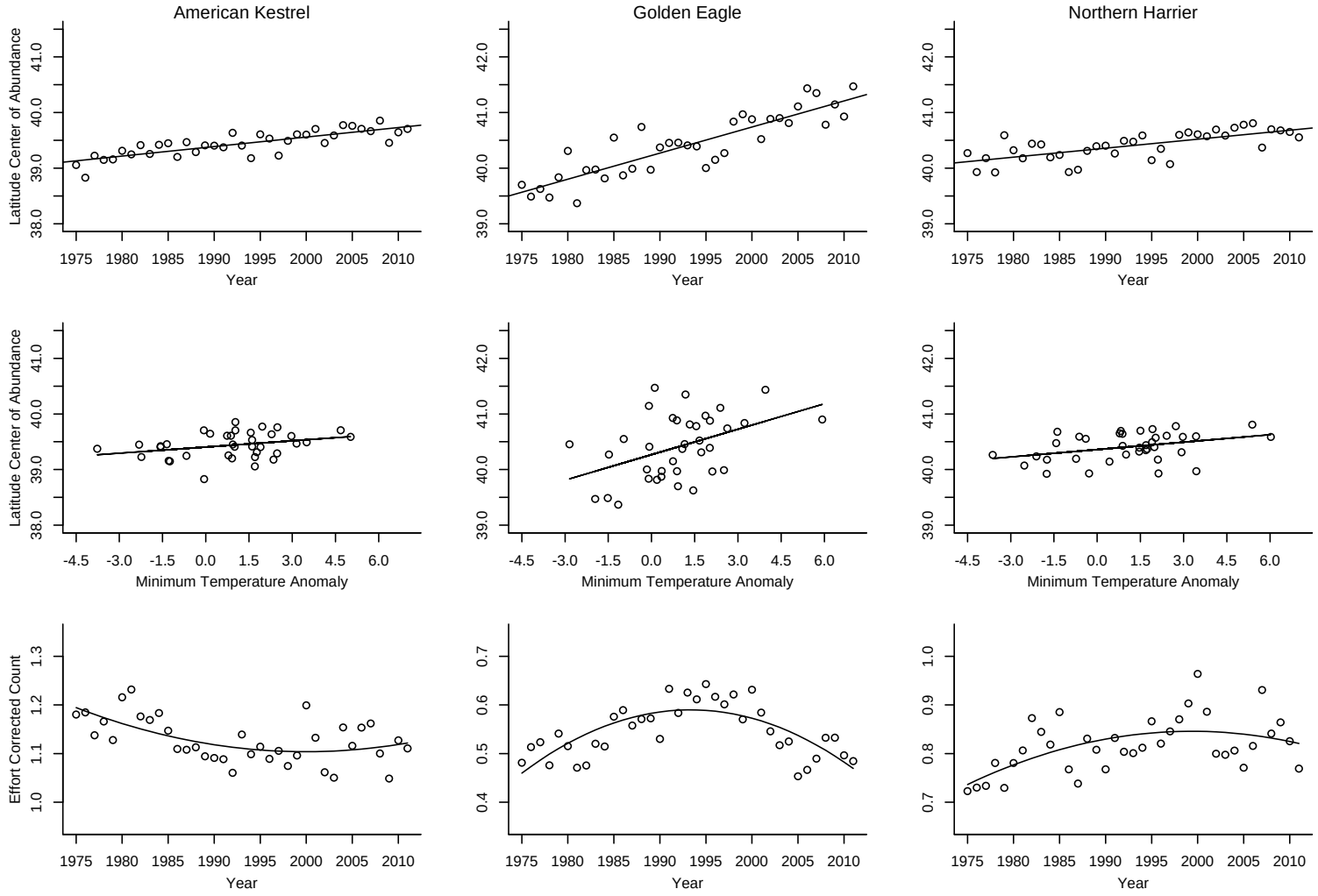
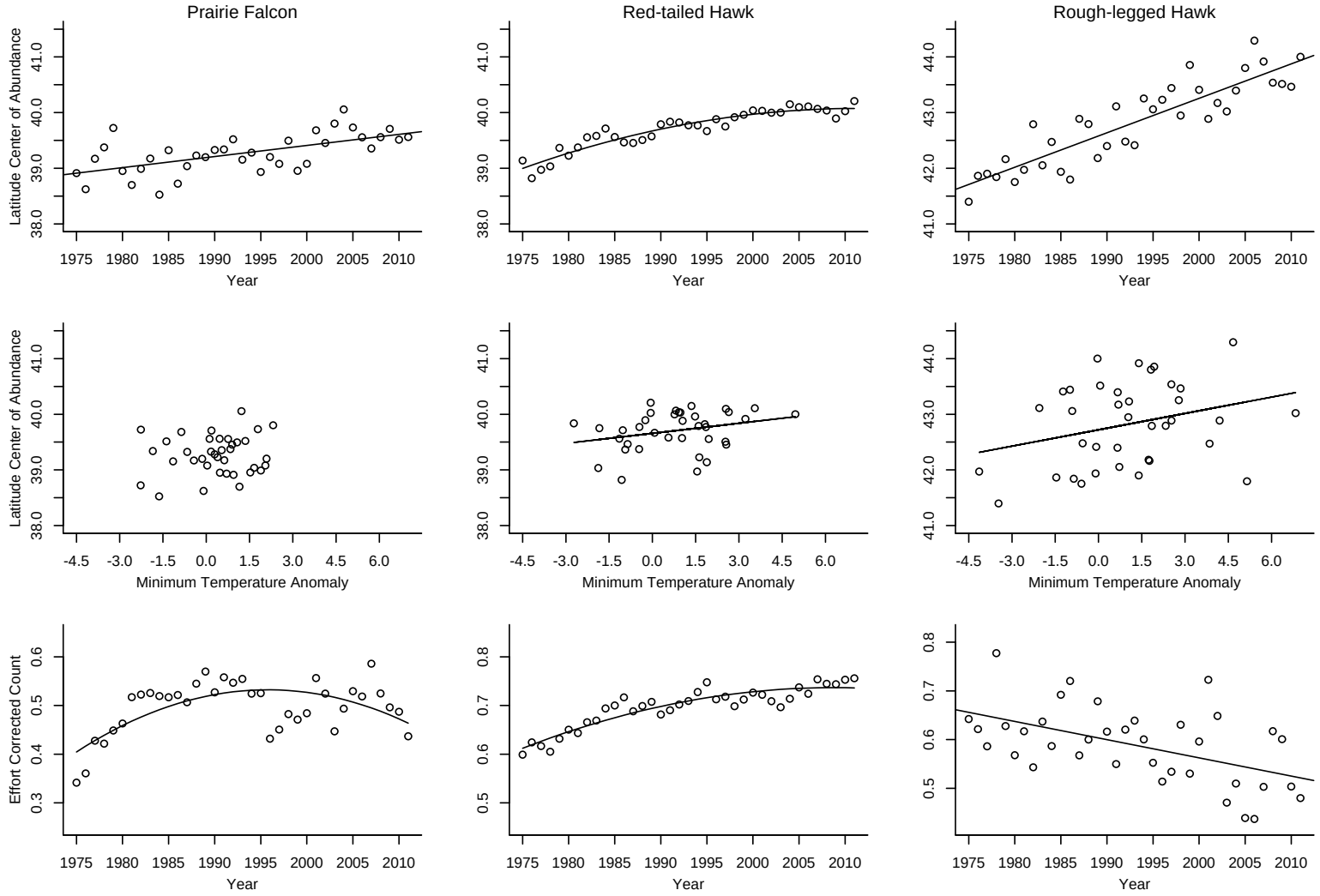

American Kestrel
Golden Eagle
Northern Harrier
Latitude Center of Abundance
Effort Corrected Count
Year
Minimum Temperature Anomaly

Figure 1.1 continued.



CHAPTER 2: FLEXIBLE HABITAT USE MAY FACILITATE REGIONAL CLIMATE CHANGE RESPONSES IN WINTERING RAPTORS

Abstract

There is widespread evidence that multiple drivers of global change, such as habitat degradation, invasive species, and climate change, are impacting wildlife. Understanding how these drivers interact or affect species may be difficult because effects depend on the magnitude and duration of environmental changes and the life history of the organism. In addition, different environmental threats may be evaluated and managed at different spatial scales. I used a historical dataset from 1991-1994 and current information from 2010-2012 to examine whether wintering raptor occupancy patterns were consistent with regional changes in distribution and climate and/or habitat conditions within a local management unit, the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA). I predicted that if local populations reflected regional trends, then raptor occupancy within the NCA would be higher compared to historical estimates and birds would show different habitat use over time. Alternatively, if local populations were determined by habitat conditions, then I predicted raptor occupancy within the NCA would be lower compared to historical estimates and birds would show little change in habitat use. Results support the hypothesis that northward distribution shifts in response to warming climates were influencing wintering raptor populations in southwest Idaho to a greater extent than local habitat degradation because wintering raptors in recent years had higher occupancy rates compared to the historical

time period and habitat suitability decreased as the proportion of invasive grasses increased and native shrubs decreased over time. Higher occupancy was associated with changes in habitat use compared to historical use patterns. Organisms in degrading landscapes that are flexible in their habitat use may be better able to respond to continental forces such as climate change. Results support the hypothesis that habitat or prey specialists may be poorly equipped to handle such rapid, large-scale global change. Further, Grinnellian niche models that forecast species response to climate change by mapping current habitat use to forecasted vegetation types should consider plasticity in habitat use and changes in life history cost and benefit trade-offs.

Introduction

Anthropogenic activities are now recognized as drivers bringing about global change (Chapin et al. 2000), and there is increasing evidence that habitat degradation (Wilcove et al. 1998, Debinski and Holt 2000, Fahrig 2003), invasive species (Knapp 1996, Bradley 2010), and climate change (Parmesan and Yohe 2003) impact species distributions and abundance. The relative importance of each of these drivers may vary by species (Jiguet et al. 2007, Rubidge et al. 2011) or across ecosystems (Bradley 2010) depending on the magnitude and duration of environmental change. In addition, drivers may have interactive effects on species distributions (Rubidge et al. 2011) and abundance (Van Horne et al. 1997, Steenhof et al. 1999), but these relationships can be difficult to evaluate.

The relative effect of these drivers also depends on spatial scale (Kim et al. 2008, Chapter 1). For example, local or continental climatic factors such as temperature and precipitation (Kim et al. 2008), regional habitat change caused by increased urbanization,

or both (Zuckerberg et al. 2011) may influence local abundance patterns. Highly mobile animals, such as birds, may change their distribution as they stay within a shifting "climate niche" (Tingley et al. 2009). However, changes in climate and habitat may lead to changes in cost and benefit trade-offs for species. There is empirical evidence supporting the hypothesis that species using a variety of habitat types may be better suited to cope with environmental changes (Sundell et al. 2012). Other species that exhibit specialist habitat affinities may experience steeper population declines (Julliard et al. 2003), especially if these affinities are not phenotypically plastic.

The Great Basin sagebrush steppe is an example of an ecosystem undergoing rapid change as a result of anthropogenic activities. Shrub-steppe may be one of the most threatened ecosystems in North America for a variety of reasons including expanding human development and the presence of invasive species (Knick et al. 2003). Invasive annual plants including cheatgrass (*Bromus* tectorum) and medusahead (*Taeniatherum caput-medusae*) now infest millions of hectares in this region and their negative ecological impacts lead to a reduction in native biodiversity, modification of ecosystem processes, and a massive alteration of the fire regime (Steenhof et al. 2006, Beck et al. 2009, Bradley 2010). Populations of Piute ground squirrel (*Spermophilus mollis*; formerly Townsend's ground squirrel *Spermophilus townsendii*) are unstable and occur at lower densities in cheatgrass and other invasive communities (Yensen et al. 1992, Steenhof et al. 2006). The climate of the Great Basin has also changed significantly with increased temperatures since 1979 (Intergovernmental Panel on Climate Change 2007). There has also been a decline in the proportion of precipitation that falls as snow and snow cover since 1984 (Harpold et al. 2012). Climate change is expected to continue and

the Great Basin is projected to warm further and experience increased precipitation as rain instead of snow (Abatzoglou and Kolden 2011).

Predatory raptors use specific habitat types because prey availability differs between habitat types and food may be limiting during periods of high energetic demand such as reproduction, migration, or overwintering (Marzluff et al. 1997); thus, raptors are susceptible to environmental change. For example, major fires causing negative vegetation and prey effects on a territory reduced reproductive success of golden eagles (*Aquila chrysaetos*; Kochert et al. 1999) post-burn, and increased anthropogenic landscape features avoided by rough-legged hawks (*Buteo lagopus*) reduced local wintering populations (Schmidt and Bock 2005). Raptors are also responding to climate change: raptors wintered farther north during warm winters (Olson and Arsenault 2000; Kim et al. 2008; Chapter 1) and have shifted their distributions farther north over time (La Sorte and Thompson 2007, Chapter 1). These continental distribution shifts in response to climate change have resulted in regionally increasing winter raptor populations in the Great Basin (Chapter 1). Distribution shifts may result from shorter migration distances (Heath et al. 2012), increased winter residency, or both (Goodrich et al. 2012), allowing raptors to reduce migratory costs and stay closer to their breeding grounds.

Given raptor responses to climate change and their dependence on prey availability, they are an interesting group for studies about the interactive effects of climate and habitat change. I used an historical dataset from 1991-1994 and current information from 2010-2012 to examine whether wintering raptor occupancy patterns were consistent with regional changes in distribution and climate or habitat conditions

within a specific management area, the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA). I predicted that if local populations of American kestrels (*Falco sparverius*), golden eagles, northern harriers (*Circus cyaneus*), prairie falcons (*Falco mexicanus*), red-tailed hawks (*Buteo jamaicensis*), and rough-legged hawks reflected regional trends, then raptor occupancy within the NCA would be higher compared to historical estimates and birds would show difference in habitat use over time. Alternatively, if local populations were determined by habitat conditions, then I predicted raptor occupancy within the NCA would be lower compared to historical estimates, with little change in habitat use in remaining raptor populations.

Methods

Study Area

The U.S. Bureau of Land Management's Morley Nelson Snake River Birds of Prey National Conservation Area is located approximately 32 km south of Boise, in southwestern Idaho, USA. The NCA is approximately 196,000 ha along 130 km of the Snake River and is part of the larger sagebrush steppe ecosystem of the Great Basin of North America (U.S. Department of the Interior 2008). The NCA contains the largest concentration of non-colonial nesting raptors in the world (Kochert and Pellant 1986). Common raptors that breed and overwintered in the NCA included American kestrels, golden eagles, northern harriers, prairie falcon, and red-tailed hawks (Kochert and Pellant 1986). The NCA wintering populations of these species contained a mix of resident and migrant birds. Of these, prairie falcons were the only species whose northern breeding limit did not extend into the boreal forest of Canada and Alaska (Steenhof 1998). Rough-legged hawks were the only common wintering raptor that did not breed in the NCA, as

their breeding range was located in the Alaskan and Canadian arctic (Bechard and Swem 2002). Thus all wintering rough-legged hawks in the NCA were most likely migrants.

Native habitat in the NCA is characteristic of shrubsteppe and was dominated by big sagebrush (*Artemisia tridentata*), green rabbitbrush (*Chrysothamnus viscidiflorus*), shadscale (*Atriplex confertifolia*), and winterfat (*Krascheninnikovia lanata*), along with native grasses (*Pseudoroegneria spicata*, *Poa secunda*; U.S. Department of the Interior 1996). Over the decades, numerous wildfires destroyed approximately 50% of the native shrub habitat (Kochert and Pellant 1986) creating areas now dominated by exotic grasses (*Bromus tectorum*) and forbs (i.e. *Salsola tragus*, *Sisymbrium altissiumum*). Topography of the NCA is generally flat or rolling with a few isolated rocky outcroppings (Steenhof et al. 1999). Climate was semi-arid with hot, dry summers and cool, wet winters when most of the annual 15-25 cm of precipitation fell. Livestock grazing occurred throughout the NCA and the Idaho Army National Guard conducted training within the NCA on the 56,000 ha Orchard Training Area (OTA).

Field Methods

I obtained historical data for wintering raptors across 190 point count sites within the Integration Study Area (ISA) used in the Bureau of Land Management/Idaho Army National Guard (BLM-IDARNG) research project (U.S. Department of the Interior 1996). The ISA encompasses roughly two-thirds of the northwest NCA on the north side of the Snake River (Figure 2.1). Watson et al. (1996) surveyed point counts from 15 November through 28 February during the 1991, 1992, and 1993 winters. They identified point count sites via a stratified random sample by first excluding areas within a 1-km buffer of the study area, on either side of the OTA boundary, and north of the Snake

River canyon rim. They divided the study area into 12 regions (six each located within and outside the OTA) distinguished by their distance from the Snake River and from the East-West midline within the ISA. A total of 200 point count sites were identified and the number of sites selected from within each region was proportional to the size of that region. They reduced the final number of sites selected to 190 based on accessibility and visibility. Watson et al. (1996) visited sites during the morning, midday, and afternoon for a total of 3 visits during each winter to account time of day effects (Bunn et al. 1995). They surveyed all sites once before a second round of visits was made leaving roughly 1 month between survey visits at a specific site. They conducted point counts for 20 min centered on a 1,000 m radius circle and alternated intensive 90 degree scans using 10x42 binoculars with 360 degree naked eye scans. They did not conduct point counts during heavy precipitation or when visibility was less than 1,000 m.

I conducted wintering raptor surveys at these same historical point count sites during the 2010-11 and 2011-12 winters. Because of logistical constraints during this time, I surveyed approximately half of the sites 3 times during each winter to total 3 visits at all 179 sites during both winters combined (n = 100 in 2010 and n = 79 in 2011). Because of burning after the 2010 winter (n = 10) and accessibility issues (n = 1), 11 historical sites were not surveyed in 2011. I surveyed point count sites using the same sampling protocol as Watson et al. (1996), however I altered the timing of survey visits in 2010 and 2011. I modified the timing of survey visits by reducing the duration between visits to better account for raptor availability (the probability that a raptor can be detected during a count) as previous work suggested this would enhance the ability to detect species' with large home ranges (MacKenzie and Royle 2005). I surveyed one of the 12

sections of sites 3 times within one week before moving on to another sampling section. I also surveyed 50 sites in 2011 using both historical and the modified sampling schemes to assess how the difference in duration between visits affected detectability (probability of sampling, availability, and detectability) of each raptor species. If duration between visits did not affect detection estimates I assumed constant detectability between the historical and modified sampling periods. Given evidence for climate change, I also examined whether the 15 November - 28 February historical study season coincided with the current timing and duration of winter. I collected local winter weather data from 1990 to 2011 including weekly heating degree days and snow cover from the Boise Airport (KBOI) weather station located approximately 15 km north of the NCA (www.wunderground.com).

I obtained habitat data by estimating the proportion of vegetation cover within 1,000 m (314 ha) of a point count site. To maintain consistency with previous work (Watson et al. 1996, Knick et al. 1997) I categorized the habitat around sites into 6 types based on dominant vegetation cover: agriculture – any irrigated or developed land; sagebrush - ≥5% sagebrush cover; rabbitbrush - ≥5% rabbitbrush cover; shadscale - ≥5% shadscale cover; winterfat - ≥5% winterfat cover; invasive - ≤5% shrub cover. I used a plot frame method (Daubenmire 1959) to train my eyes to assess percent vegetation cover in a shrub stand and then mapped vegetation cover at each site (henceforth referred to as 'habitat field data').

I used a combination of satellite and aerial imagery from 1991, 2010, and 2011 to map my habitat field data. I obtained 3 Landsat 5 TM images from March to July for both 1991 and 2010 (Path 41/Row 30; 30 x 30 m pixels, 0.09 ha; U.S. Geological Survey

2012) along with the 2011 National Agricultural Imagery Program (NAIP) Digital Orthoimagery Series of Idaho (1 x 1 m, 0.0001 ha; natural color and false color; Idaho Geospatial Data Clearinghouse 2012). I did not use Landsat 5 TM images from 2011 because of a lack of cloud-free imagery. For the 2010 habitat analysis I outlined my habitat field data in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA). I only outlined habitat polygons that were at least 90 x 90 m in size (equivalent to 3 x 3 Landsat pixels) to limit classification of small vegetation patches (Congalton and Green 2009). I was conservative in outlining my habitat data and ambiguous habitat field data was not mapped digitally. To increase the sample size of each habitat category, I used the 2011 NAIP imagery to manually outline additional habitat polygons within the NCA. I was also conservative around edges of additional habitat polygons to compensate for pixel size differences between NAIP and Landsat imagery. For the 1991 habitat analysis I compared habitat field data collected in 2011 to that collected in 1991 by Watson et al. (1996) to find areas of little change, including areas already infested with invasives. I digitally outlined these habitat polygons along with additional polygons obtained by comparing 1991 Landsat imagery to 1991 habitat field data. I also used 1991 Landsat imagery to outline additional habitat polygons within the NCA.

For both 1991 and 2010, I used a layer stacking procedure to compile 18 calibrated Landsat images (Singh and Glenn 2009). I used 6 bands each (Landsat 5 TM bands 1, 2, 3, 4, 5, and 7) from 3 images taken between March and July of each year to capture the full spectral variability of invasive plants. The Landsat images were calibrated to at-sensor reflectance using ENVI. I used the Geospatial Modelling Environment v. 0.7.2.1 RC2 (GUI; www.spatialecology.com/gme/, accessed on 8 Sep

2012) to randomly select habitat polygons for training and accuracy (Congalton and Green 2009) in a supervised maximum-likelihood habitat classifier. I used the remote sensing program ENVI 5.0 (ITT Visual Information Solutions, Boulder, CO) for all further habitat classification. I was unable to accurately classify the rabbitbrush and shadscale habitat categories and therefore assigned each pixel in the 18-band Landsat composites to 1 of 4 collapsed habitat categories: 1) sagebrush-rabbitbrush complex; 2) shadscale-winterfat complex; 3) invasive; and 4) agriculture. Because sagebrush and winterfat also exist as a complex, I assigned these habitats to categories based on which shrub type covered the majority of a site. My habitat classification technique of the NCA had an overall accuracy of 80% and 81% in 1991 (Table 2.1) and 2010 (Table 2.2), respectively (kappa values ranged from 0.68 to 0.65). After the classification was complete, I used the Geospatial Modelling Environment to calculate habitat proportions within a 1,000 m radius surrounding each point count site.

Data Analysis

Unless otherwise noted, I used an information-theoretic approach with second-order Akaike's information criterion (AIC_c; Burnham and Anderson 2002) and software from the R Development Core Team (2012) for all statistical analyses. I used package unmarked to assess whether detection was different between my two sampling schemes by creating a dummy survey covariate for sampling scheme and comparing this to the null model. I assumed constant detection between time periods if the effect of sampling scheme was within 2 ΔAIC_c of the null model. Given climate change patterns, I evaluated whether the timing or duration of winter had changed from 1 November 1990 to 28 March 2012 to ensure a reliable winter sample in both historical and recent years. I

defined my winter weather metrics in the following ways: 1) winter duration as the number of weeks between the first and last weeks with ≥ 200 heating degree days, and 2) winter median as the median week of winter duration. One heating degree day is accumulated for every whole degree Fahrenheit that the mean daily temperature is below 65° F (18.3° C; Steenhof et al. 1997), and a 200 heating degree day week corresponds to an average weekly temperature of roughly 36° F (2.2° C).

I then compared raptor occupancy using naïve occupancy across all sites surveyed from 1991 to 1993 and from 2010 to 2011 because low detection probabilities (less than 0.15) in the 1990s created unreliable occupancy estimates (MacKenzie et al. 2002). I used generalized linear mixed models from the lme4 package for all further raptor occupancy and habitat use analyses. I created species-specific independent models for raptor presence or absence by including sampling period (historical or recent) as a predictor variable, the month of February as a fixed variable, and point count site as a random variable to assess whether raptor occupancy depended on sampling period. I used the month of February as an *a priori* fixed variable (i.e., a block) as this is roughly the time when Piute ground squirrels begin to emerge from their burrows, and I had reason to believe this affected the occupancy of raptors.

Habitat differences were non-normal so I ran a non-parametric Wilcoxon signed-rank test for each of my 4 habitat categories to assess proportion of habitat change at point count sites. I only analyzed changes in occupancy and habitat use when naïve occupancy was >0.10 in a given sampling period to avoid difficulties with small sample sizes. I created species-specific independent models for raptor presence or absence by including sampling period (historical or modified), habitat type, and the interaction

between sampling period and habitat as predictor variables, the month of February as a fixed variable, and point count site as a random variable to assess whether habitat use depended on sampling period. I created separate model sets for each vegetation type because of multicollinearity between proportions of vegetation within sample plots. When the interaction between sampling period and habitat type was the top model, I used independent models for each sampling period and habitat type to predict raptor occupancy. When the interaction between sampling period and habitat type was not the top model, I combined both sampling periods to predict raptor occupancy in a given habitat type. For each model in a given set I calculated an AIC_c value along with an Akaike Weight (Burnham and Anderson 2002). I assessed raptor occupancy and habitat use from these models using parameter estimates and 85% confidence intervals (85% CI) to achieve full AIC compatibility (Arnold 2010). I considered habitat covariates with 85% CI that did not overlap 0 as biologically informative.

Results

I assumed a constant detection probability between the historical and modified sampling techniques because the effect of sampling scheme was within 2 ΔAIC_c of the null model for all 4 species (Table 2.3). I also found no change in winter duration (ω = 0.35, β = −0.06, 85% CI = −0.14, 0.02) or the median week of winter (ω = 0.23, β = 0.01, 85% CI = −0.03, 0.05). After controlling for the effect of February, I observed an increase in occupancy between sampling periods for golden eagles (ω = 0.73, β = 0.32, 85% CI = 0.09, 0.55), northern harriers (ω = 1.00, β = 1.60, 85% CI = 1.40, 1.79), prairie falcons (ω = 1.00, β = 1.48, 85% CI = 1.25, 1.72), and rough-legged hawks (ω = 1.00, β = 1.08, 85% CI = 0.89, 1.27; Fig. 2.2). American kestrel and red-tailed hawk

historical occupancy was ≤0.10, however raw data suggested they were also more common in recent years compared with historical data (Table 2.4).

I observed changes in vegetation cover within point count sites between 1991 and 2010 (Fig. 2.3). Median sagebrush-rabbitbrush and shadscale-winterfat cover decreased by 3.91% (T = 5208, P = 0.002, 95% CI = −6.61, −1.72) and 5.88% (T = 2753, P < 0.0001, 95% CI = −8.41, −3.89), respectively. Median invasive and agriculture cover increased by 11.59% (T = 13565, P < 0.0001, 95% CI = 8.00, 15.60) and 0.69% (T = 6037, P < 0.0001, 95% CI = 0.30, 1.08), respectively (Fig. 2.3).

Changes in raptor occupancy within habitat types varied over time by species and habitat type (Fig. 2.4). Golden eagle occupancy within agriculture differed between sampling periods (1990s: β = −0.98, 85% CI = −2.26, 0.30; 2010s: β = −4.84, 85% CI = −8.20, 1.48; Fig. 2.4a), although occupancy tended to be lower with higher proportions of agriculture. Golden eagle occupancy was positively associated with sagebrush-rabbitbrush (β = 1.05, 85% CI = 0.71, 1.38), but negatively associated with invasive (β = −1.12, 85% CI = −1.47, −0.78) during the entire study period (historical and modified). Golden eagle occupancy was not associated with shadscale-winterfat during the entire study period (β = 0.39, 85% CI = −0.01, 0.79). Northern harrier occupancy was positively associated with agriculture, although this relationship was more pronounced in recent years (1990s: β = 1.78, 85% CI = 0.82, 2.74; 2010s: β = 3.27, 85% CI = 2.22, 4.34; Fig. 2.4b). Harrier occupancy within invasive (1990s: β = −1.20, 85% CI = −1.65, −0.75; 2010s: β = −0.57, 85% CI = −1.06, −0.10) and shadscale-winterfat (1990s: β = −2.11, 85% CI = −2.84, −1.38; 2010s: β = −0.45, 85% CI = −1.24, 0.34) differed between sampling periods, however these relationships tended to be negative. Harrier

occupancy within sagebrush-rabbitbrush also differed between sampling periods (1990s: β = 1.71, 85% CI = 1.31, 2.10; 2010s: β = 0.04, 85% CI = −0.46, 0.53) with no recent occupancy association. The direction of prairie falcon occupancy estimates within invasive (1990s: β = −0.66, 85% CI = −1.13, −0.20; 2010s: β = 0.38, 85% CI = −0.16, 0.92; Fig. 2.4c) and agriculture (1990s: β = 1.90, 85% CI = 1.09, 2.71; 2010s: β = −2.10, 85% CI = −3.75, −0.45) were opposite between sampling periods. Prairie falcon occupancy was not associated with shadscale-winterfat (β = 0.11, 85% CI = −0.72, 0.94) or sagebrush-rabbitbrush (β = −0.06, 85% CI = −0.41, 0.29) in either study period. The direction of rough-legged hawk occupancy estimates within invasive (1990s: β = −0.24, 85% CI = −0.62, 0.14; 2010s: β = 1.27, 85% CI = 0.67, 1.88; Fig. 2.4d) and agriculture (1990s: β = 1.86, 85% CI = 1.12, 2.60; 2010s: β = −0.64, 85% CI = −2.09, 0.81) were also opposite between sampling periods. Rough-legged hawk occupancy within sagebrush-rabbitbrush decreased between sampling periods (1990s: β = −0.02, 85% CI = −0.39, 0.36; 2010s: β = −0.99, 85% CI = −1.64, −0.35). Rough-legged hawk occupancy was negatively associated with shadscale-winterfat (β = −0.62, 85% CI = −1.02, −0.22) during both study periods. Finally, American kestrel (β = 8.23, 85% CI = 5.48, 10.99) and red-tailed hawk (β = 4.29, 85% CI = 0.27, 8.32) occupancy was positively associated with agricultural in the 2010s, but showed no association with other habitat types.

Discussion

All wintering raptors showed evidence for an increase in occupancy from the 1990s to the 2010s in the NCA. The amount of native shrub cover at sample sites

decreased between 1991 and 2010 while open areas dominated by invasive grasses and forbs increased. All raptor species exhibited changes in habitat use between the two time periods, however the degree of change varied by species. Together, these results supported my hypothesis of regional population responses to climate change, and not local vegetation change, influencing wintering raptor populations in southwest Idaho. The results also supported the prediction that as local raptor occupancy increased habitat use patterns would change. This may suggest that the overall costs for raptors occupying alternative habitats do not out-weigh the benefits conferred by favorable climatic conditions.

Changes in local wintering raptor populations in the NCA are consistent with studies of regional population changes in the Great Basin (Chapter 1). Many raptors in western North America are wintering further north, partly because of range shifts facilitated by warming winters (Chapter 1). These northward shifts may result from a combination of decreased migration distances or migratory "short-stopping", and increased wintering residency. Studies have demonstrated a decrease in fall raptor migration distances associated with warming temperatures (Heath et al. 2012). Raptors may benefit from decreased migration distances through a reduction in migratory costs and the ability to stay closer to, or on the breeding grounds, through winter. For many species including merlins (*Falco columbarius*; Espie et al. 2000) and American kestrels (Strasser 2010) early arrival to the breeding grounds has been shown to positively predict reproduction success.

Within my study area, the ability of raptor species' to shift their occupancy patterns to reflect changes in landscape composition may have partially mediated their

apparent regional response to climate change. For example, golden eagles exhibited the smallest occupancy increase with little change in their habitat use between study periods. The lack of habitat use change by golden eagles, coupled with their positive association to sagebrush-rabbitbrush and negative association with invasive may be one reason why their change in occupancy was lower than other species. Previous work in the NCA showed that golden eagles were capable of shifting to a broader diet during declines in their primary prey (black-tailed jackrabbits *Lepus californicus*; Steenhof and Kochert 1988) in the nesting season. However, if golden eagles are unable to use different habitat types to find prey then they may be more susceptible to continued habitat degradation within the NCA, regardless of flexibility in diet. Population levels of wintering golden eagles may eventually decline if primary prey and native shrub habitat continues to degrade from encroaching invasive plant species.

Northern harriers, prairie falcons, and rough-legged hawk all exhibited large occupancy increases and showed substantial changes in habitat use between study periods. As regional wintering raptor populations in some northern areas such as the Great Basin increase because of distribution shifts facilitated by climate change (Chapter 1), these three species may even increase in areas with degrading landscapes by having the ability to shift their habitat use. Another hypothesis is that the large occupancy increase created a carrying capacity in preferred habitats with a finite area, causing other individuals to occupy sub-optimal habitats (Bowers & Matter 1997, Hanski & Ovaskainen 2000) because of inter or intraspecific interactions (Schmidt and Bock 2005, Olson 2006). This hypothesis seems unlikely however, especially in instances where associations with particular habitats were opposite between time periods. In recent years

for example, prairie falcons had a negative association with agriculture and a nearly positive association with invasive. These associations were opposite those of the historical period. Horned larks (*Eremophila alpestris*) and western meadowlarks (*Sturnella neglecta*) are important components of prairie falcon winter diets (Steenhof 1998), and although I did not collect data on prey availability or consumption, I regularly observed prairie falcons hunting large horned lark flocks in open grassland. During the breeding season, horned larks of the sagebrush-steppe prefer areas with reduced shrub cover and more invasives (Earnst and Holmes 2012), and have exhibited increased abundance in post-fire areas (Earnst et al 2009). The abundance of wintering horned larks in invasive areas is unknown, but may be a contributing factor in the observed change in prairie falcon habitat use.

Northern harriers and rough-legged hawks prey on small mammals (Koivula and Viitala 1999, Littlefield and Johnson 2005); yet despite this similarity, each species exhibited different habitat use over time, possibly because of differences in their tolerance of anthropogenic landscape features (Berry et al. 1998). My results suggest that compared to the 1990s northern harriers in the 2010s occupied areas dominated by sagebrush less but increased their use of agricultural areas around the edge of the NCA. Unlike areas high in cheatgrass cover and fragmented sagebrush, some agricultural areas with more edge habitat may contain higher densities of small mammals than surrounding areas (Renwick and Lambin 2011, Sullivan et al. 2012). Tolerance of harriers to anthropogenic features (Berry et al. 1998, Cardador et al. 2012) may have allowed this species to increase use in agriculture. Although rough-legged hawks also occupied sagebrush habitat less in the 2010s compared with the 1990s, they are now negatively

associated with this habitat type and use agricultural areas less than historically. In contrast to harriers, rough-legged hawks are now positively associated with invasive habitat. Previously research has suggested rough-legged hawks avoid human settlements (Berry et al. 1998, Schmidt and Bock 2005). Although agricultural habitat around the edges of the NCA increased slightly, if the amount of other anthropogenic features including new home development has increased during this same time then this increased anthropogenic infrastructure may have been one reason why rough-legged hawks are now using agricultural areas less than in historical times (1990s). Another cause of this change in habitat use may have been increased competitive exclusion because of interspecific interactions (Schmidt and Bock 2005, Olson 2006) with winter populations of red-tailed hawk (Chapter 1), which are increasing in agricultural areas.

Although habitat specialists are more susceptible to population declines from large-scale drivers such as climate change and habitat degradation (Julliard et al. 2003, Jiguet et al. 2007); habitat use over the long-term should be considered. If I had just assessed data from 2010 and 2011, I may have concluded that northern harriers were the most specialized habitat user as they showed a strong positive association with agriculture. I might have incorrectly concluded that harriers were more susceptible to population declines. By assessing habitat use and its change over time I have put forward the hypothesis that it was not habitat specialization per se that influenced a species response to climate change. Instead, the ability of a species to be flexible in its habitat use allowed it to exploit the changing landscape in the face of global climate change. Future studies should explore how prey populations are responding to changing predation

pressure given the large increase in raptor presence and use of different habitat types I observed.

Management Implications

In our changing world, the ability to parse out the relative contributions of climate and landscape change on populations is becoming increasingly important. In this study, winter raptor populations may be increasing in northern regions despite continued landscape degradation in the Great Basin sage-steppe ecosystem. The ecological consequences of this increase on overall ecosystem health are unknown but warrant future study. Increases in raptor populations are facilitated by range shifts partly because of warming winters (Chapter 1). As species decrease migration distances and increased winter residency, northern conservation areas and public lands such as the Morley Nelson Snake River Birds of Prey National Conservation Area will become increasingly more important for population persistence. Many researchers have wondered about the potential management effects and implications of climate change, and my research provides evidence that organisms flexible in their habitat use stemming from changing landscapes appear better able to respond to global and continental forces such as climate change. The implication is that less flexible habitat or prey specialists, such as the golden eagle, may not be as well equipped to handle such large-scale forces. Further, niche models that forecast a species distribution response to climate change (Doswald et a. 2009) by using current habitat preferences to forecasted vegetation types (Heikkinen et al. 2010) should consider flexibility in habitat preferences and other life-history strategies.

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Table 2.1. Error matrix for the 1991 supervised maximum likelihood classification of the Morley Nelson Snake River Birds of Prey National Conservation Area. Matrix numbers correspond to number of pixels in each of 4 habitat categories: sagebrush/rabbitbrush complex (sage), shadscale/winterfat (shad), invasive (invs) and agriculture (agri). Numbers in parentheses represent the number of habitat polygons used as reference or classified data.

		1991 Reference Data				
		sage (57)	shad (90)	invs (50)	agri (25)	Row Total
1991 Classified Data	sage (82)	39765	735	15176	2	55678
	shad (97)	2094	20210	12020	2	34326
	invs (66)	4489	7982	107416	6092	125979
	agri (31)	14	0	701	24760	25475
	Column Total	46362	28927	135313	30856	241458
		Overall Accuracy = 79.6%, Kappa = 0.677				
		Producer's Accuracy		User's Accuracy		
	sage	85.8%		71.4%		
	shad	70.0%		58.9%		
	invs	79.4%		85.3%		
	agri	80.2%		97.2%		

Table 2.2. Error matrix for the 2010 supervised maximum likelihood classification of the Morley Nelson Snake River Birds of Prey National Conservation Area. Matrix numbers correspond to number of pixels in each of 4 habitat categories: sagebrush/rabbitbrush complex (sage), shadscale/winterfat (shad), invasive (invs) and agriculture (agri). Numbers in parentheses represent the number of habitat polygons used as reference or classified data.

		2010 Reference Data				
		sage (299)	shad (100)	invs (153)	agri (15)	Row Total
2010 Classified Data	sage (100)	64620	343	23003	39	88005
	shad (127)	1703	12596	2889	3	17191
	invs (50)	18473	6754	156424	435	182086
	agri (22)	507	19	4619	12067	17212
	Column Total	85303	19712	186935	12544	304494
		Overall Accuracy = 80.7%, Kappa = 0.646				
		Producer's Accuracy		User's Accuracy		
	sage	75.8%		73.4%		
	shad	63.9%		73.3%		
	invs	83.7%		85.9%		
	agri	96.2%		70.1%		

Table 2.3. Model sets predicting probability of detection in relation to sampling scheme (method) for four wintering raptor species in the Morley Nelson Snake River Birds of Prey National Conservation Area, 2011. Models are ordered according to the support received from Akaike's information criterion (AIC_c) and from Akaike weights (w_i); k = number of parameters; $\Delta AIC = AIC_{ci} - \text{minimum } AIC_c$.

Species	Model	k	AIC_c	ΔAIC	ω_i
golden eagle	null	2	181.16	0.00	0.68
	method	3	182.71	1.54	0.32
northern harrier	method	3	380.57	0.00	0.61
	null	2	381.49	0.91	0.39
prairie falcon	null	2	282.27	0.00	0.74
	method	3	284.31	2.04	0.26
rough-legged hawk	null	2	294.07	0.00	0.72
	method	3	295.96	1.89	0.28

Table 2.4. Species, average raw count total per year (n/year and n), number of birds per site (n/site), and naïve occupancy (Ψ) with 95% confidence intervals of wintering raptors at 175 commonly surveyed point count sites in the Morley Nelson Snake River Birds of Prey National Conservation Area, Idaho. Sites were surveyed three times each year from 1991 through 1993 and three times each year in 2010 or 2011.

Species	1991-1993			2010-2011		
	n/year	n/site	Ψ	n[a]	n/site	Ψ
American kestrel[b]	8	0.05	0.05	65	0.38 ± 0.41	0.20 ± 0.18
golden eagle	69.33 ± 26.56	0.40 ± 0.15	0.28 ± 0.14	87	0.49 ± 0.56	0.34 ± 0.24
northern harrier	75.67 ± 79.35	0.43 ± 0.45	0.31 ± 0.23	222	1.25 ± 1.39	0.65 ± 0.52
prairie falcon	44.00 ± 25.21	0.25 ± 0.14	0.22 ± 0.14	119	0.67 ± 0.54	0.51 ± 0.60
rough-legged hawk	78.00 ± 78.20	0.45 ± 0.45	0.31 ± 0.31	191	1.05 ± 3.98	0.53 ± 0.86
red-tailed hawk	19.67 ± 36.20	0.11 ± 0.21	0.10 ± 0.19	40	0.24 ± 0.83	0.16 ± 0.63

[a]175 total sites were surveyed between 2010 and 2011.

[b]Site-specific data only available from 1991, 2010, and 2011 for American kestrels.

Figure 2.1. The Integration Study Area (ISA) and randomly selected points within the Morley Nelson Snake River Birds of Prey National Conservation Area that represent the center of a 1,000 m radius point count survey area. From the BLM-IDARNG research project (US Department of the Interior 1996).

Figure 2.2. Probability of naïve raptor occupancy from generalized linear mixed models with sampling period as a predictor variable (1991-1993 or 2010-2011), month of February as a fixed variable, and point count site as a random variable for wintering golden eagles (A), northern harriers (B), prairie falcons (C), and rough-legged hawks (D) in the Morley Nelson Snake River Birds of Prey National Conservation Area, Idaho. Probability of occupancy was back-transformed after holding the effect of the fixed variable February at zero.

Figure 2.3. The average ground cover proportion with 95% confidence intervals of 4 habitat categories within a 1,000 m radius of point count sites (n = 190) from a Landsat maximum likelihood classification of the Morley Nelson Snake River Birds of Prey National Conservation Area, Idaho, 1991 (circles) and 2010 (triangles).

Figure 2.4. Probability of naïve raptor occupancy from generalized linear mixed models with sampling period (1991-1993 or 2010-2011) and habitat type as predictor variables, month of February as a fixed variable, and point count site as a random variable for wintering golden eagles (A), northern harriers (B), prairie falcons (C), and rough-legged hawks (D) in the Morley Nelson Snake River Birds of Prey National Conservation Area,

Idaho. Grey and black lines and dots represent the 1990s and 2010s, respectively when an interaction was present between habitat use and sample period. When an interaction was not present, solitary black lines represent 1990s and 2010s combined habitat use. 85% confidence intervals (dashed lines) indicate there was a predictive relationship between habitat type and raptor occupancy. Probability of occupancy was back-transformed after holding the effect of the fixed variable February at zero.

Figure 2.1.

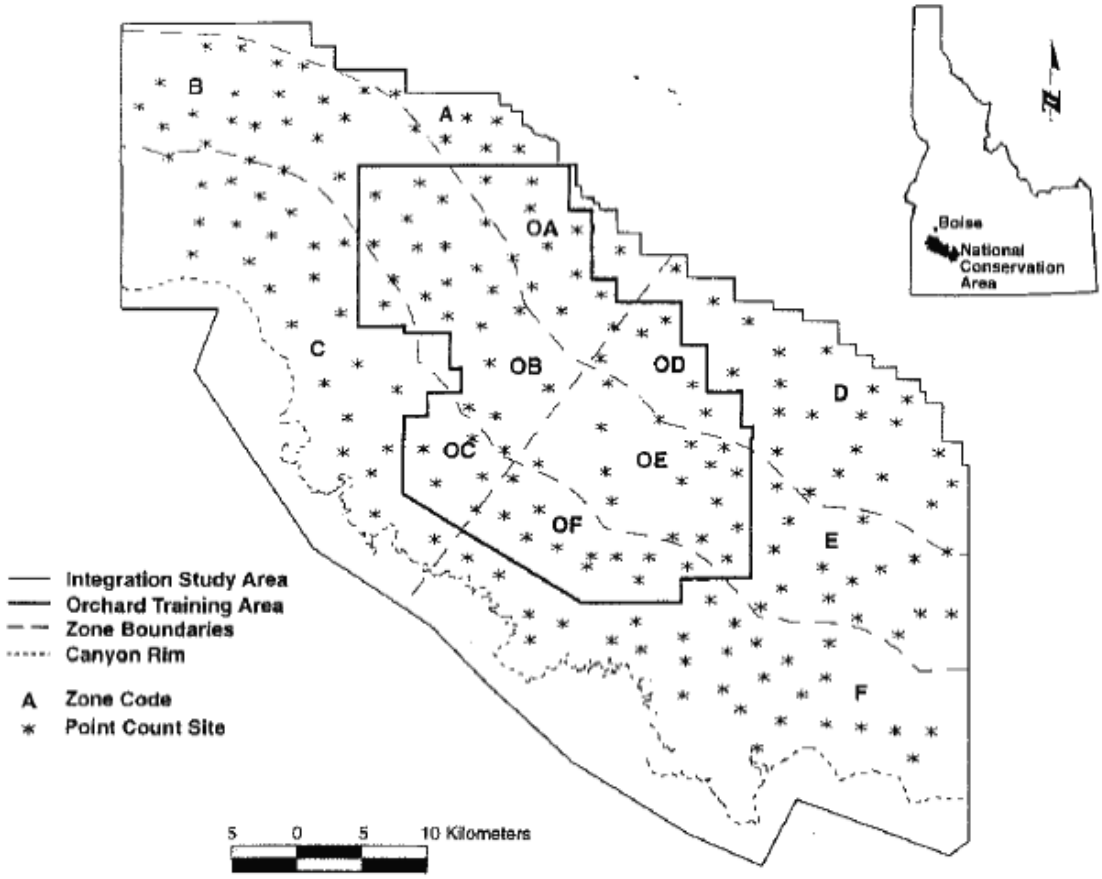

B
A
OA
C
OB
OD
D
OC
OE
OF
E
F
Integration Study Area
Orchard Training Area
Zone Boundaries
Canyon Rim
A Zone Code
Point Count Site
5 0 5 10 Kilometers
N
Boise
National
Conservation
Area

Figure 2.2.

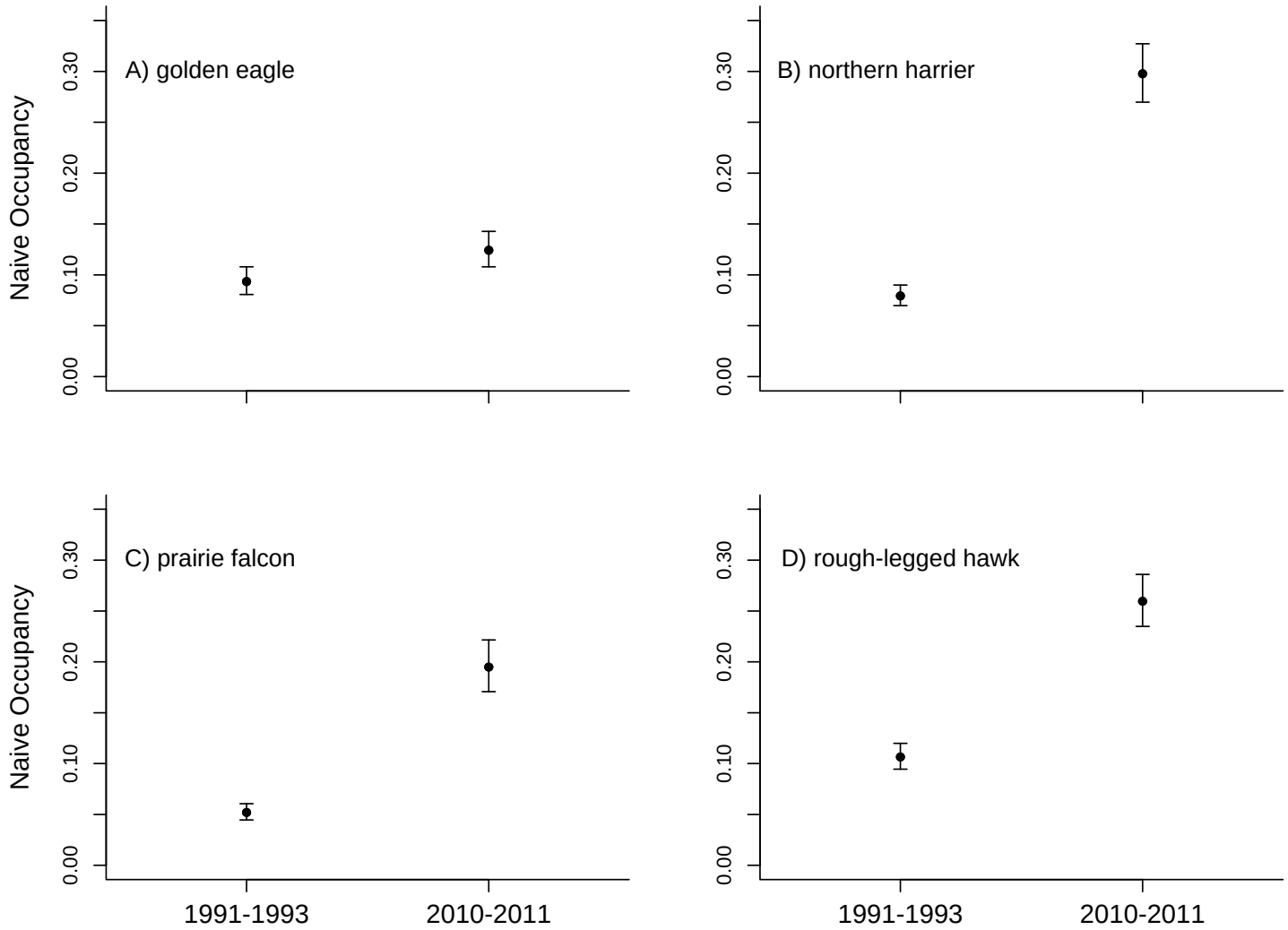

A) golden eagle
B) northern harrier
C) prairie falcon
D) rough-legged hawk
Naive Occupancy
0.00
0.10
0.20
0.30
1991-1993
2010-2011

Figure 2.3.

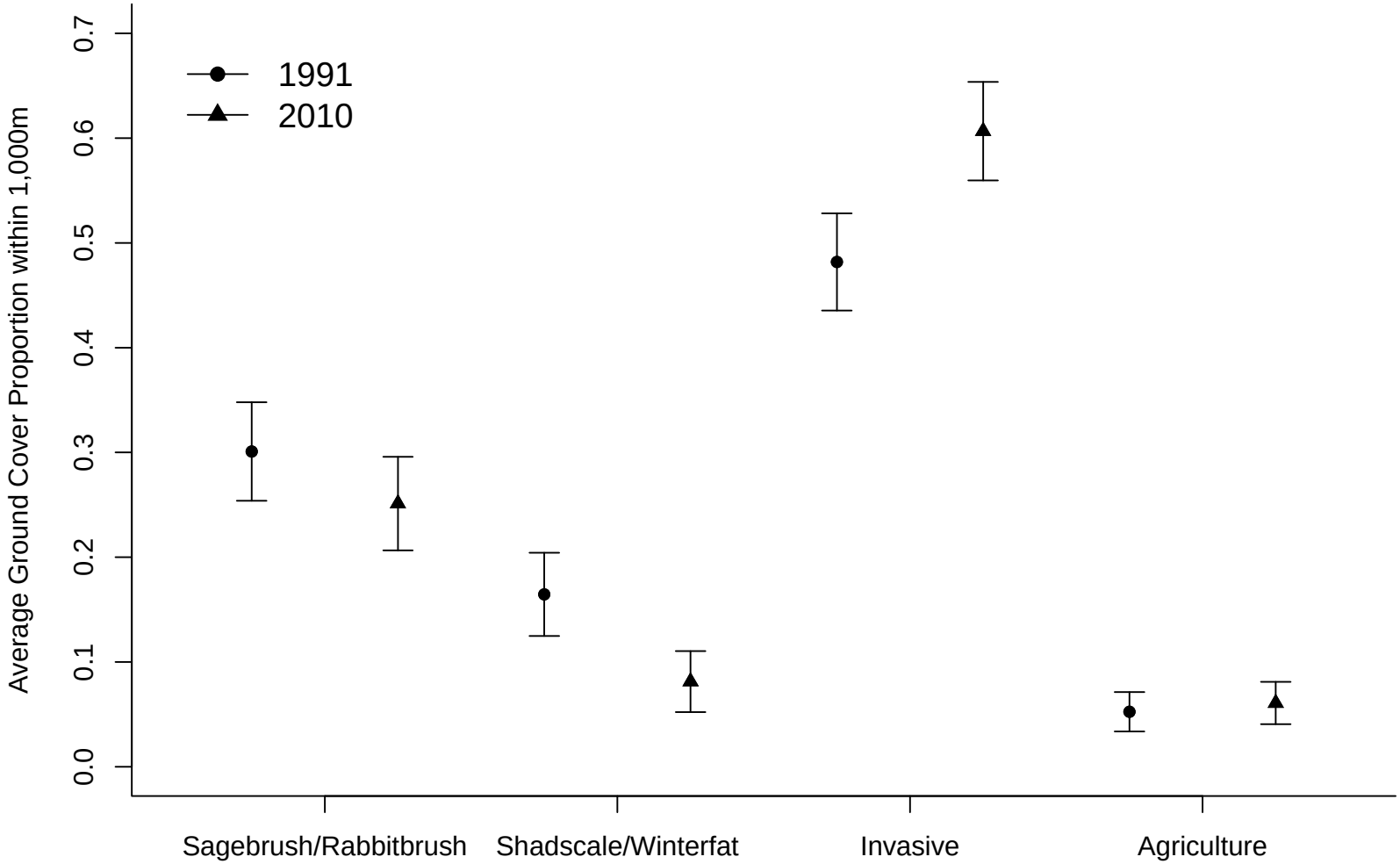

1991
2010
Average Ground Cover Proportion within 1,000m
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Sagebrush/Rabbitbrush
Shadscale/Winterfat
Invasive
Agriculture

Figure 2.4.

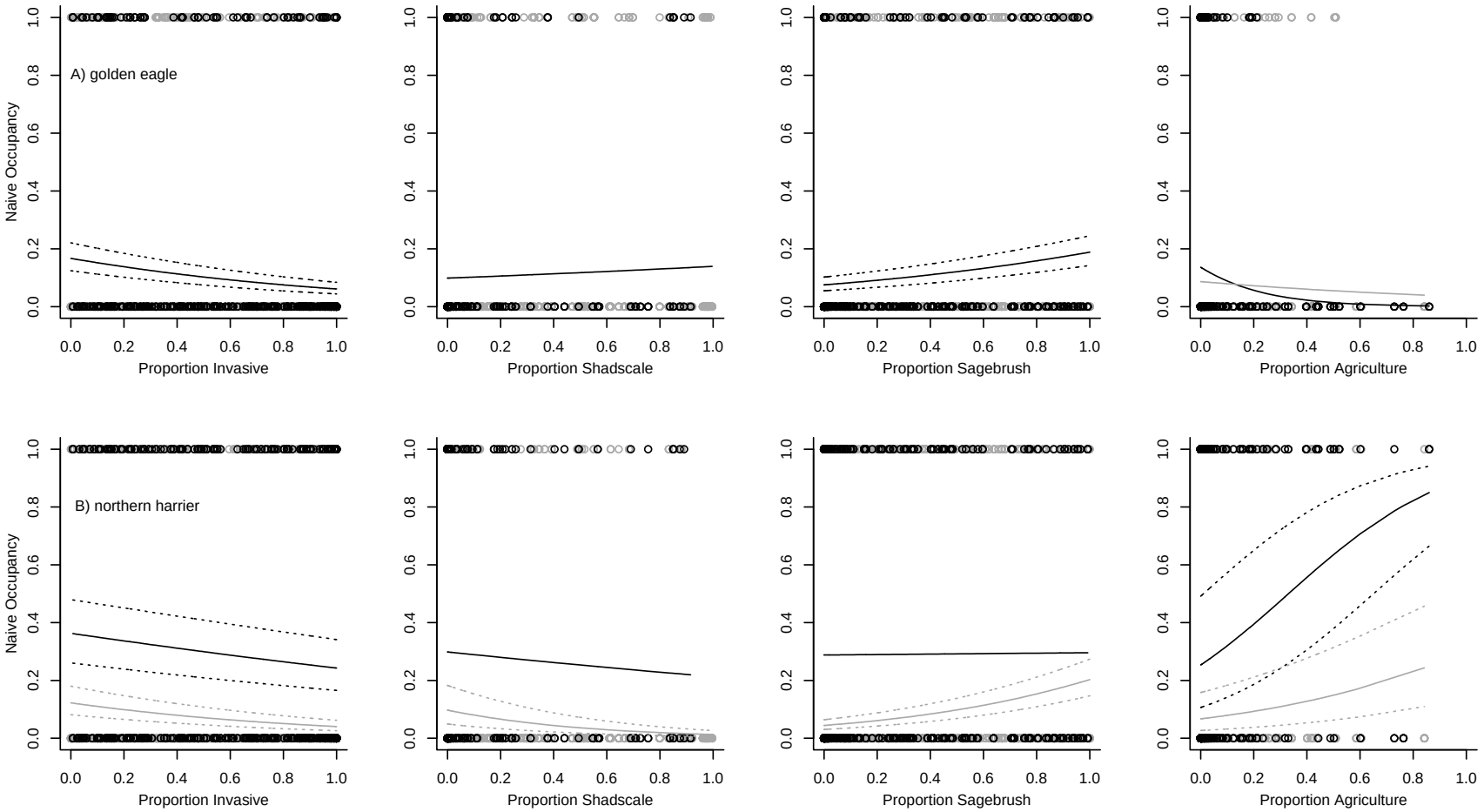
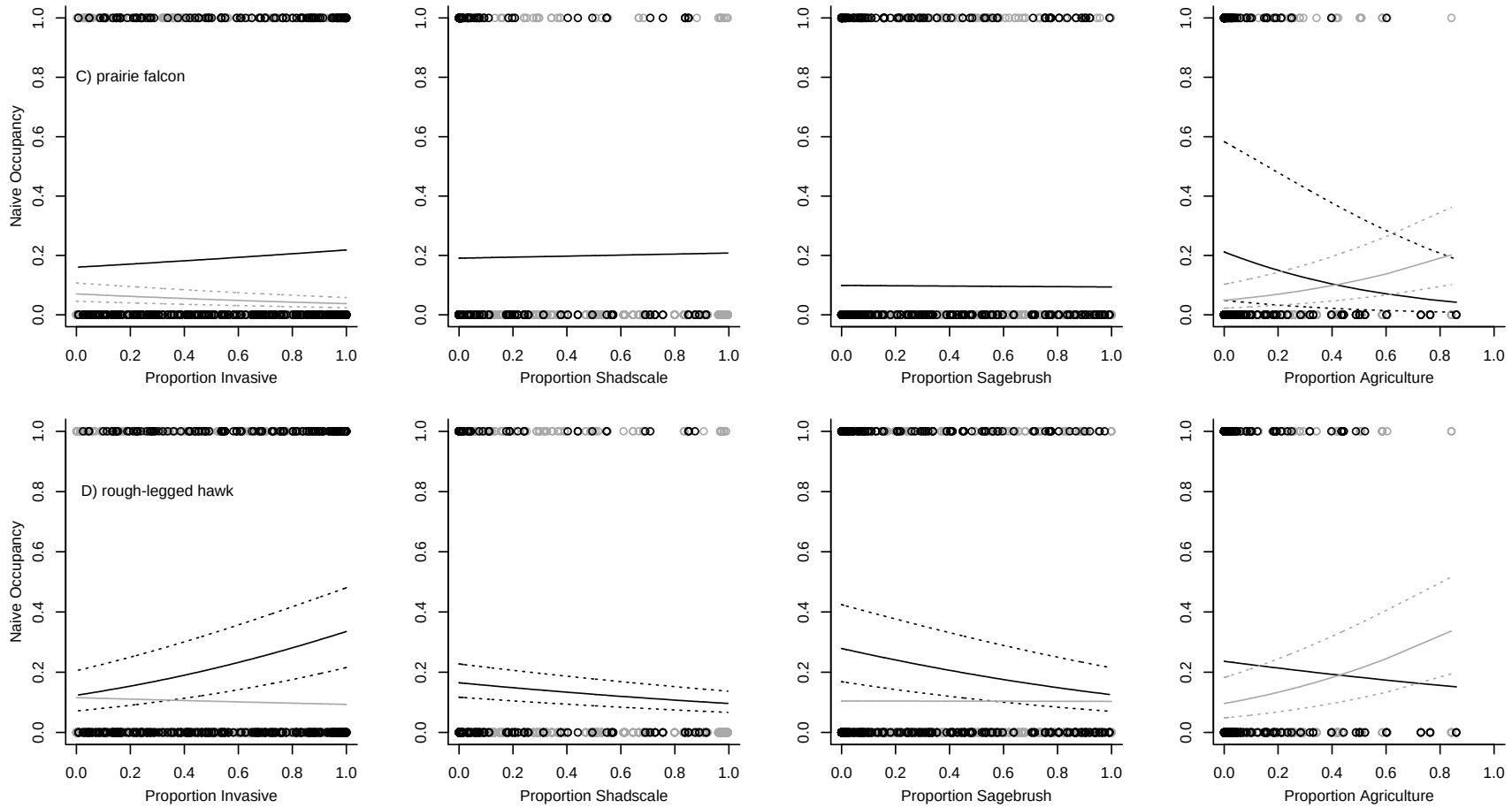

A) golden eagle
B) northern harrier
Naive Occupancy
Proportion Invasive
Proportion Shadscale
Proportion Sagebrush
Proportion Agriculture
0.0
0.2
0.4
0.6
0.8
1.0

Figure 2.4 continued.



CONCLUSION

Assessing population responses to changing environmental conditions, including habitat and climate change, should encompass multiple spatial scales and time periods whenever possible. Choosing a single spatial scale or time period can limit biologically informative inferences. Local and regional population responses may differ from each other, and from continental responses. Without knowledge that winter raptor distributions were shifting north across western North America (Chapter 1), the locally increasing raptor populations I observed in southwest Idaho (Chapter 2) would have been difficult to understand. Inclusion of long-term data or data from multiple time periods also helps scientists grasp how population responses change over time. Habitat use of wintering raptors in my study area varied across time periods (Chapter 2) and helped to elucidate the differential response of raptors to climate and habitat change. Because of budgetary and logistical challenges it can be difficult to monitor population responses at multiple spatial scales and time periods. However, resources are available such as public data from long-term, broad-scale citizen science based projects (i.e. the Christmas Bird Count) to alleviate this limitation.

Using publically available Christmas Bird Count (CBC) data, I discovered a northward shift in the wintering distribution of six western North American raptor species in Chapter 1. These northward shifts were predictive of some regional population indices in Bird Conservation Regions (BCR). However, some regional population indices were not explained by northward shifts and warrant further discussion. American kestrels and

golden eagles are two species thought to be declining across much of their range (Hoffman and Smith 2003, Smith et al. 2008). Across western North American CBCs, I found evidence for an initial range-wide population decline in American kestrels from 1975 to 2000. However, the kestrel population appeared to stabilize and may even be increasing after the year 2000. Regionally, the negative population trends observed in the Southern Rockies/Colorado Plateau and Coastal California BCRs were best explained by changes in population over time. Given this information, researchers and management agencies in these regions should focus their work to determine the causes behind wintering population declines.

My results of an overall decline in golden eagle western populations since the mid-1990s corroborate previous research (Hoffman and Smith 2003, Smith et al. 2008). This is concerning given the historical sensitivity of eagles to environmental disturbance (Watson et al. 2002) and the potential threats golden eagles now face from wind power (Smallwood and Thelander 2008), lead poisoning (Stauber et al. 2010, Kelly et al. 2011), and others. I found competing evidence between distribution shifts and population changes explaining indices for regionally declining populations of golden eagles. However, BCRs that were partly explained by population change were more often located towards the periphery of the golden eagles winter range (i.e. the Central Mixed-grass Prairie and Sonoran and Mohave Desert BCRs). This may suggest that golden eagle winter populations are declining in areas outside their core range or from individuals that migrate further distances from the breeding grounds (i.e. juvenile), contributing to the recent decline in the overall western North American golden eagle winter population.

In Chapter 2 I used historical and recent data to assess changes in raptor occupancy and habitat use over time at a local level in the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA), Idaho. Given the large increase I observed in occupancy of some wintering raptors coupled with continued habitat degradation begged the question: what is the response of the raptor prey base in the shrub-steppe food web of the NCA? Habitat change alone is not always the best predictor of population sizes, and some studies have suggested food-web models were better predictors of response to habitat change (see Gotelli and Ellison 2006). I realized the importance of considering the entire food web, and while I did not directly assess prey fluctuations as part of my shrub-steppe system, some views on prey population responses are offered. The implications of changing habitat associations for wintering raptors are that they are now exploiting either the same or a different prey resource in a new habitat. How prey populations are responding to the changing and increasing predation pressure of the NCA is unknown, but research has shown potential consequences may include reduced prey populations (Morris et al 2011) and changes in prey habitat use (Sundell et al 2012).

Golden eagles only showed a marginal occupancy increase while also being the most inflexible habitat user, with little change over time. Golden eagles have been shown to diversify their diet during black-tailed jackrabbit declines (Steenhof and Kochert 1988), and if they have done this, what has been the effect on other prey taxa within their preferred native shrub communities? All eagles are known to scavenge, and golden eagles were observed scavenging on stillborn cattle fetuses and placenta from livestock

grazed in the NCA. In much the same way bald eagles do, perhaps this population is now relying more heavily on scavenging to survive the non-breeding months.

Prairie falcons may be becoming more reliant on horned larks populations for winter survival, however little is known about wintering horned lark populations and the potential carry-over effects of this prey resource into the breeding season. Further, how late-winter emergent ground squirrel populations are affecting the fitness of breeding falcons given continued habitat degradation is also unknown. Northern harriers strong preference for agricultural areas may also be a preference for an increased amount of edge habitat created by these anthropogenic features. How this large increase in wintering harriers is affecting small mammal communities in exurban areas is not well understood. Finally, rough-legged hawks in the NCA are now using open invasive areas more than their availability, and were the only species to do so. Small mammal diversity and density decline in invasive landscapes (Hanser and Huntly 2006), so why rough-legged hawks are selecting this habitat is puzzling. Given these changes in habitat use coupled with raptor population increases more research is needed to determine how prey populations are responding, and how these responses are affecting the body condition of raptors in the breeding season, and their reproductive success (fitness).

It appears that area already dominated by cheatgrass and other invasive plant species within the sagebrush-steppe ecosystem are here to stay (Davies et al. 2011). Thus, more research is needed to determine how animal and plant populations are responding and possibly adapting to landscapes dominated by invasive plants. The use of invasive dominated areas, a potentially sub-optimal habitat, by rough-legged hawks may have negative carry-over effects into the breeding season if individuals surviving to the

breeding season are in poor body condition (Sherry and Holmes 1996). Results from Chapter 1 suggest the size of wintering populations of rough-legged hawks in western North America appear to be declining, at least partly because of large northward range shifts affecting adequacy of long-term Christmas Bird Count surveys in the northern wintering range of the species. Research is now needed to determine the status of breeding populations given these declines, their use of sub-optimal winter habitat, and possible increased competitive exclusion (Schmidt and Bock 2005) from increasing populations of larger conspecifics such as red-tailed hawks (Chapter 1).

In summary, I found evidence that some winter raptor populations are increasing in northern regions despite continued landscape degradation in the Great Basin sage-steppe ecosystem. These increases were facilitated by range shifts partly because of warming winters. My research over multiple spatial-scales and time-periods provided some evidence that organisms flexible in habitat use associated with changing landscapes appear better able to respond to global and continental forces such as climate change. How northern ecosystems are responding to increasing wintering raptor populations is unknown but warrants future study. As species winter further north and habitat continues to degrade and fragment, northern conservation areas and public lands such as the Morley Nelson Snake River Birds of Prey National Conservation Area and others are likely to become refugia for population persistence. The long-term implications of such events will require further study.

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